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A Monograph of the Nearctic Plagiochilaceae

Part I. Introduction and Sectio I. Asplenioides.*

RUDOLF M. SCHUSTER

Duke University, Durham[1]

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* Additional parts will appear in subsequent issues. The references will be cited in the last part.

[1] Present address: University of Massachusetts, Amherst, Mass. The final revision of the manuscript and the final field work were done while in residence at the Highlands Biological Station, Highlands, N. C.

INTRODUCTION

The present study owes its genesis to an attempt to identify the accumulated collections of *Plagiochila* made by the author in the years 1946-1953, utilizing the existing literature. It was to be expected that the pioneer paper by Evans (1896) would have outlived much of its utility. Evans, furthermore, in subsequent papers (1905, 1914) described additional species and modified his earlier species concepts. Moreover, a recent treatment exists (Frye and Clark, 1944:433-455) which has not materially advanced our comprehension of the group, and in several points actually represents a regression from the papers of Evans. A modern revision is thus necessary, particularly since *Plagiochila* includes such a high percentage of endemics, thus making it impossible for the American student to use the reliable, standard European floras (Macvicar, 1926; Müller, 1905-16; 1950-56).

Although the initial concern of the author was to prepare a reliable key to our Plagiochilaceae, the literature was found so unsatisfactory that any understanding of the species necessitated a study of the type material. The summer of 1952 was spent in studying type and cotype material deposited in the herbarium of the New York Botanical Garden. Type material of all species described from America north of Mexico and some from Central America was examined, as well as type material of *"Mylia" cuneifolia*. Of all the types detailed illustrations were made, and descriptive notes as well as a key to the species prepared. The next step was to become thoroughly familiar with living material to ascertain the ecological characteristics of the species, as well as their cytological features. In August, 1952, therefore, a 2100 mile trip was taken through the Appalachian Plateau region—the center of distribution of the genus for North America, followed (December-January 1952-53, 1953-54, 1954-55, 1955-56) by several long trips to tropical Florida—the region of recent invasion by various tropical Plagiochilae, and (May-Sept. 1955) to Ellesmere Island. From May 1953-July 1956 more than twelve collecting trips were made to all parts of the Southern Appalachians, and the summer of 1957 was spent in the Southern Appalachians; during 1953-56 the coastal portions of the southeast, north of Florida, were investigated. This concentrated investigation of the Plagiochilaceae followed a decade of more casual study of the group, with study of the tropical species during the winters of 1950-51 and 1951-52 in tropical and subtropical Florida; study of the species along the Gulf Coast during the summer of 1951; study of the Appalachian species during May, 1951.

The extensive field work has served to acquaint the author with all the nearctic species of the family (excepting *Pedinophyllum interruptum* and *Plagiochila "alaskana"*). Familiarity with the species as living, dynamic entities, rather than dry, dead herbarium specimens has made it possible to study not only the ecological features of the species, but also the characteristics of the living cell of each species.

In the Plagiochilaceae, as in other families, extranuclear cytology has proved to be significant in defining more critically the species concept. Furthermore, field study of the species—of large quantities of material *in situ*—has impressed upon the author the great diversity in reproductive patterns that exists within the family. The varying types of asexual reproduction (and their absence in some species) have proved not only of considerable biological interest, but also of great value in indicating affinities of the species—as well as in the practical problem of determination of sterile material. In fact, the cytology and mode of reproduction of the various species of *"Mylia"* and *Plagiochila* appear to be among the most significant taxonomic characteristics. Since the most recent attempt by Carl (1931a) to subdivide the portmanteau genus *Plagiochila* is sufficiently unsatisfactory in some details, and the species groups he recognizes sometimes ill-defined (when based on geographical and not morphological criteria), a new attempt, based in part on the cytological and biological criteria emphasized above, is of potential value. In the much smaller genus "*Mylia*" (s. lat.) a similar situation exists; hence the present work attempts to exploit, at least in part, the radically different asexual reproductive patterns in classifying this form-genus. The author urges most strongly that living material be utilized as far as possible in future work on the Plagiochilaceae, so that the cytological features, as well as the mode of asexual reproduction, may be carefully noted. Accumulation, during the next several decades, of a large body of such data should make possible, eventually, a sound division of the plagiochiloid genera into sections (and possibly subgenera). Although these data are needed most acutely in *Plagiochila,* they are almost equally important in *"Mylia"* (s. lat.) where we also find radically different types of oil-bodies and differing modes of asexual reproduction.

In many species of both genera, sexual reproduction is unknown. In fact, it appears probable that some of these species (such as *"Mylia" cuneifolia*) no longer possess the ability to reproduce sexually, at least regionally. Furthermore, the asexual reproductive modes appear to be ancient in their origin; hence it may be assumed that species with differing types of asexual reproduction are only distantly related, while species with identical modes of such reproduction are probably more closely allied. In other groups of Hepaticae we find a similar constancy of reproductive pattern within the genus (and often within the family). For instance, in the closely allied families Scapaniaceae and Lophoziaceae, the dominant method of asexual reproduction is by 1-2, rarely 3-4-celled fasciculate gemmae originating from the leaf-margins. By contrast, the entire suborder Porellinae (Porellaceae, Frullaniaceae, Lejeuneaceae) possesses a tendency to develop marginal discoid gemmae, or similar discoid gemmae arising from the leaf-surface — but never produces gemmae in fasciculate masses. The suborder Radulinae is closely similar to the Porellinae in this characteristic. Both the Radulinae and Porellinae show a well-developed tendency towards development of a second asexual reproductive mode: caducous leaves. This never occurs in the Scapaniaceae and Lophoziaceae, with the exception of *Acrobolbus rhizophyllus*. Such differences, positive and negative,

are part of the chain of circumstantial evidence the phylogenist must consider in any attempt to develop a sound and presumably phylogenetic classification.

As will be developed, the Plagiochilaceae possess a wide range of asexual reproductive patterns, ranging from fasciculate 2-celled gemmae (*Mylia*, s. str.) to brood-plantlets or propagula of the leaf-surface, to caducous leaves and leaf-lobes, to fragmenting leaves. Therefore, though the asexual reproductive modes are sufficiently diverse in the family to make it impossible to use them for family circumspection, they become of primary importance in intrafamiliar classification.

Finally, it should be emphasized that the present work can be regarded only as a tentative effort. Even though study of the types and the living plant has served to more sharply define the taxa occurring in the area treated, two major types of study remain to be carried out, both of which potentially may serve to considerably modify the present treatment, namely: 1) Culture work with living materials, and 2) study of the various genera from a synthetic, world-wide viewpoint. The first type of study may result in some synonymy—or in further splitting of species; the second would certainly result in some nomenclatural changes, a few of which are hinted at in the following pages. Integration of our species with those of the neotropics and the east Asiatic area has been attempted. Further study of this type is much needed, and will probably result in additional nomenclatural changes. The names of some of our species of *Plagiochila*, therefore, must remain an open matter, since several of these may on further study prove to be only disjunct populations (or subspecies) of more widely distributed neotropical or oceanic species. Since the main concern of the present study has been to establish firmly the reality (or lack of reality) of the established nearctic entities, their relationship to extra-territorial ones must in several cases remain in abeyance until more adequate herbarium facilities are available.

More study of variation within the species is also needed. The analysis of variability in the *Plagiochila ludoviciana-miradorensis* complex presented in this paper is merely a beginning towards this type of analysis. I have attempted to maintain a reasonably conservative course in recognizing varieties and forms (which are non-geographical intraspecific taxa) and subspecies (which I regard as major, geographical segments of polytypic species). Such intraspecific groupings as I recognize must be subject to further scrutiny. Their present utility lies largely in affording us some means of ordering the bewildering variability exhibited by many species.

As an example of the problems which the worker on the genus faces, the history of several of our species may be briefly reviewed. Such a review will prove useful if it serves no other purpose than to give pause to the taxonomic worker on the genus who is faced with "new" taxa in poorly investigated areas. The tendency, in such cases, is always to describe these as new, increasing with each added description the burden placed on future workers. These species are *P. semidecurrens*, *P. sharpii*, *P. yokogurensis*, and *P. japonica*. In the first case (*P. semidecurrens*) the writer had to cope with the problem of the two "species," *P. alaskana* and *P. fryei*, known only from Alaska. These were pat-

ently closely allied to the Appalachian *P. sharpii.* A two-month study of this problem revealed that (a) *P. alaskana* and *P. fryei* were synonymous with the Japanese *P. semidecurrens* var. *grossidens;* (b) *P. semidecurrens* var. *grossidens* as defined by Hattori included a plant not identical with the type of this; this plant had been earlier described by Hattori as *P. semidecurrens* var. *yakusimensis;* (c) the *P. semidecurrens* var. *yakusimensis,* from Japan, proved to be very close to the Appalachian *P. sharpii,* and probably represents only a race of it.

In the case of *P. yokogurensis,* the situation was even more chaotic. In studying a series of eastern Plagiochilae, a fragile-leaved plant was repeatedly found, both in the field and in herbaria. This plant had been misdetermined (Evans, 1896; Blomquist, 1936; Frye and Clark, 1944; Jacobs, 1953) for a variety of unrelated nearctic species, and was found in herbaria (and listed in the American literature) under the names of *P. virginica, P. ludoviciana, P. austini,* etc. On the basis of its fragile leaves, it was given the manuscript name *fragilifolia.* A careful perusal of the literature on the Mexican and neotropical flora did not reveal any American relatives. Prolonged study indicated that the Japanese *P. yokogurensis* came very close to the American plant. Investigation of a series of specimens revealed that Japanese and American plants could be separated only by several "tendencies" such as a slight difference in the form of the teeth of the leaves. On that basis, the American plant was regarded as a subspecies, or race, of *P. yokogurensis,* described on a succeeding page.

The final case involves a peculiar, aciculate-toothed, shiny plant first sent to the writer by R. L. McGregor, from Arkansas. More copious collections, made by L. E. Anderson, soon became available. This plant, assigned to the exclusively neotropical Sectio Subplanae, could not be assigned to any of the neotropical taxa. For it the manuscript name *ciliigera* was selected. In addition to the extremely slender teeth of the leaves, the finely granulose oil-bodies were particularly noted as a differential feature. Such oil-bodies had not been found in any other holarctic and neotropical species seen. In a subsequent study of the drawings of oil-bodies of Japanese Plagiochilae (in the fine paper by Hattori, 1951a), the striking and unique similarity of the oil-bodies of the Japanese *P. japonica,* to the Ozarkian *ciliigera* was noted; this led to a more careful comparison of *P. japonica* to our nearctic plant. Again, an almost overwhelming similarity — but minor, more or less constant, differences were noted, leading to a consideration of *ciliigera* as a race of *P. japonica.* This last case illustrates several points the writer wishes especially to emphasize: (a) the often fantastically wide disjunction of these ancient, early Tertiary or perhaps late Mesozoic species; (b) as a consequence, when a previously unknown *Plagiochila* is found in a given region, it is totally unsafe to preclude the possibility that the same plant will not be found in (and often has been described under several names from) geographically remote areas; (c) with 1,200 described "species," of which less than 10 percent have been adequately described or illustrated, the problem of tracking down the immediately allied species of any taxon becomes almost insurmountable. The "geographical viewpoint" so rigidly applied in the only recent work of any scope (Carl, 1931a) can scarcely lead to any alleviation of this chaotic condition.

A consequence of the chaotic condition of the systematics of *Plagiochila* is that any attempt at a correlation between the plagiochiloid flora of North America, and that of other regions, must be a hit-and-miss matter, or the result of protracted "detective work" made possible only by prolonged experience with the group. The analysis of the four species reviewed above involved almost six months' study!

Certainly, when the systematics of any genus is reduced to such a level by unmitigated species description (especially by Stephani!) a burden is laid on the shoulders of the future workers that few can assume! And in the few cases, where such an attempt is made, the results are predictable. Recent American works on the genus illustrate this point. The most glaring recent example is a paper in which out of seven listed species, five are misidentified! Perhaps the most amazing case of mistaken identity in the group is that of "*P. ludoviciana.*" The hundreds of herbarium specimens seen, labelled as this species, included the following: *P. hypnoides, P. miradorensis, P. floridana, P. dubia, P. virginica, P. yokogurensis fragilifolia,* and *P. sharpii,* as well as some specimens which actually represented true *P. ludoviciana!*

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The present study could not have been attempted without the continuous help, in all stages of its preparation, by my wife, Olga M. Schuster. I also owe a major debt to Dr. Theodor Herzog, who so kindly supplied me with portions of numerous collections of Central and South American Plagiochilae, including many types; without these, much of this study would have had to remain much less complete. Dr. S. Hattori and Mr. H. Inoue also were kind enough to supply numerous Japanese collections. Much of the initial study was done at the New York Botanical Garden, and I am indebted to Dr. D. P. Rogers and Miss Rosalie Weikert for many favors, and for the loan of much material. The stay at the New York Botanical Garden (1952) was made possible by a Faculty Research Grant from the University of Mississippi, of which I was at the time a staff member. I am also indebted to my colleagues at Duke University, in particular Drs. H. L. Blomquist and L. E. Anderson, for their efforts to show me promising collecting stations, and their criticisms of various stages of this enterprise. The publication of this monograph, in its existing form, would have been impossible without a considerable subsidy from Duke University. The cost of the included etchings has been defrayed in part by a grant from the National Science Foundation (Grant 669), and the final work on the manuscript was facilitated by a second such grant (Grant 1396), and by a Guggenheim Fellowship. The grants from the National Science Foundation, and (1955-56) receipt of a Guggenheim Fellowship also made possible much of the necessary field work. I am also indebted to the Arctic Weather Stations, United States Weather Bureau, and the Canadian Weather Bureau for facilities at Alert, Ellesmere Island, where the arctic species were studied (1955), and to the Canadian and United States Air Forces, for the necessary transportation. The Latin diagnoses were kindly prepared by Dr. A. LeRoy Andrews. For the loan of certain pertinent materials I am also indebted to Dr. A. W. Evans (Yale University), Dr. Herman Persson (Riksmuseets Paleobotaniska Avdel., Stockholm), Dr. I. Mackenzie Lamb (Farlow Herbarium), Dr. D. P. Rogers (New York Botanical Garden), and to Mrs. Mary S. Taylor, of Urbana, Ohio. I am particularly indebted to my friend, Dr. A. J. Sharp, who, on being asked for the loan of a few specimens from the University of Tennessee Herbarium, was more than gracious in lending the entire holdings in the genus *Plagiochila!* Finally, a grant from the Highlands Biological Station enabled me to make a long series of collections, after completion of the manuscript, and to subject the latter to an ultimate, intensive scrutiny. I am indebted to Prof. Thelma Howell, director of the station, both for the use of the facilities of the station, and for numerous suggestions as to profitable collecting sites.

After the body of this manuscript had been completed I was able to examine a number of Alaskan collections. For the loan of these I am indebted to Dr. T. C. Frye (University of Washington) and Dr. J. Reeder (Yale University). In the interpretation of the Alaskan material, which is in part closely affiliated with eastern Asiatic taxa, I have been aided by Dr. S. Hattori and Mr. H. Inoue. Indeed, I have largely followed their suggestions with respect to two of the North Pacific complexes, that of *P. rhizophora* and that of *P. satoi.*

After this manuscript was submitted for publication (August, 1956) H. Inoue undertook a detailed revision of the Japanese members of the family. Unfortunately the timing involved has been such that neither Mr. Inoue nor I could derive much aid from each other's efforts. He most courteously submitted a galley proof of the initial portion of his revision (January 1958); from this a few last-minute annotations, specifically noted in the body of this paper, were made. In the meantime a preliminary study which I made of the East Asiatic-Eastern American *P. yokogurensis* has appeared (Schuster, 1957). The simultaneous appearance of two *Plagiochila* floras, dealing in part with related groups of species, should at least afford future students a dual basis upon which to build.

LIMITS AND CIRCUMSCRIPTION OF THE FAMILY

LIMITS OF THE PLAGIOCHILACEAE

It would be presumptive to maintain that the term "Plagiochilaceae" as used in the present work, has more than a certain temporal value. It appears improbable that the family, as here defined, represents either a completely natural or homogeneous taxon. The family was first named, in a perfunctory way, by Buch (1936), and accepted by Evans (1940). Neither of these works included the genus *Mylia* in the Plagiochilaceae, although Müller (1939-1940) included the genus in this family. *Mylia* has been variously placed, in the Jungermanniaceae (Nardiaceae or Nardioideae), as by Buch (*loc. cit.*) and Frye and Clark (1944), or in the Harpanthaceae, as by Evans (1940). The recognition of a special group for *Plagiochila* and its allies *Mylia* and *Pedinophyllum* goes back to Joergensen (1934).

The various students of the group have all agreed that the genus *Plagiochila,* as well as such segregate genera from it as *Chiastocaulon, Plagiochilion, Plagiochilidium* belong in the Plagiochilaceae. Most students have also agreed in placing the monotypic *Pedinophyllum* into this group. Among recent students, Frye and Clark (*loc. cit.*) have placed the latter genus in a catch-all group ("Nardioideae"—considered a tribe, but nomenclatorially the name pertains to a subfamily). In this convenient portmanteau group are placed not only the genera related to *Nardia* (*e.g.,* the Jungermanniaceae of recent students), but such totally unrelated genera as *Pedinophyllum, Chiloscyphus, Mylia* and *Mesoptychia!* Buch (1936) also places *Pedinophyllum* and *Mylia* in a broadly conceived family Jungermanniaceae. Most recently Müller (1939) has re-emphasized the close relationship of *Pedinophyllum* to *Plagiochila,* stating that "die Form des Perianths, der Bau des Sporogons und des Sporogonstiels auf eine Verwandtschaft mit *Plagiochila* hinweisen.... Die Ölkörper sind ebenso wie die bei *Pla-*

giochila beschaffen, weichen also von jenen der Gattungen *Plectocolea* und *Haplozia* stark ab, weshalb die Einreihung der Gattung *Pedinophyllum* neben *Plagiochila* also die natürlichere zu bezeichnen ist." However, it deserves emphasis that Müller arrived at this conclusion after study of the oil-bodies of only one species of *Plagiochila* (*P. asplenioides*). Study of a series of species of *Plagiochila* and *Mylia* demonstrates conclusively that there is such diversity of oil-body form in these genera that the oil-bodies cannot be used as a criterion, either for inclusion of other genera within the family, or for the circumscription of the family.

The writer would also tentatively follow Müller (1939-1940) in including the "genus" *Mylia* in the Plagiochilaceae, following Joergensen (1934). Müller (*loc. cit.,* p. 184) would also include in the family the genera *Apotomanthus* Spruce, *Syzigiella* Spruce, *Plagiochilidium* Herzog, *Clasmatocolea* Spruce, and (questionably) *Tylimanthus* Mitt.

The Genus Tylimanthus Mitt.—*Tylimanthus* (or *Tylunanthus*) Mitt. deviates from all undoubted genera placed in the Plagiochilaceae in possessing a prominent, rhizoidous, swollen perigynium similar to that of *Acrobolbus* in the Lophoziaceae. As in the latter genus, the elaboration of a complex perigynium is associated with total suppression of a perianth. In these features, as well as in the total lack of underleaves, *Tylimanthus* differs markedly from "normal" Plagiochilaceae. Yet the vegetative features of *Tylimanthus* reflect an unquestionable affinity to *Plagiochila!* The development of a prostrate "caudex" from which arise leafy branches; the tendency towards *Chiastocaulon*-like postical stolons from near the point of origin of erect, leafy secondary shoots on the primary axes (see, *e.g.,* Evans, 1898, pl. 348, fig. 4); the insertion and form of the leaves, with a marked tendency towards formation of a dorsal convex fold; the form of the androecium (see Evans, 1898, pl. 348, fig. 5); the tendency towards irregular lobing of the leaf-apices and toward dentition of the leaves—these all argue forcibly for retention of the genus in the Plagiochilaceae. I have retained it as a very specialized element. Except for the absence of perceptible underleaves, such species as *T. saccatus* (Tayl.) Mitt. are virtually inseparable from *Plagiochila* in the vegetative condition. Suggestive also is the occurrence in *Tylimanthus nummularius* Herz. of caducous leaves ("fo. *deciduifolia;*" see Herzog, 1954, p. 37); such a mode of asexual reproduction is almost unknown in related families.

However, the position of the other two genera, *Clasmatocolea* and *Syzigiella,* in the Plagiochilaceae is more dubious. The former genus, after being divorced from the discordant elements introduced into it by Stephani and by Frye and Clark (such as *"Clasmatocolea" doellingeri* and *exigua*), belongs either in the Harpanthaceae (Schuster, 1958) or in the Lophocoleaceae (Grolle, 1956). As Schuster (1958) has shown, the anatomy of the seta, capsule-wall, the sporangium shape, the form of the elaters, the sculpture of the exine of the spores, the minute oil-

bodies, and the non-collenchymatous leaf-cells, as well as the obviously tetragonous perianths all indicate that no affinity to the Plagiochilaceae exists, at least as regards *"Clasmatocolea" doellingeri.*

The Genus Syzigiella Spruce.—The correct position of the genus *Syzigiella* (*"Syzygiella"*) is somewhat controversial. Carl (1931b) has emphasized the fact that it shows much similarity with opposite-leaved species included in the genus *Plagiochila* at that time (now segregated as *Plagiochilion* Hattori). The description by Herzog (Ann. Bryol. 5:85-89, figs. 2-4) of *S. plagiochiloides* Herz. is of interest, but unfortunately, an earlier *Syzigiella plagiochiloides,* was published by Spruce (1885, p. 500); Stephani (1906, p. 183) places this as a synonym of *S. manca* (Mont.) Steph. I therefore propose, for *Syzigiella plagiochiloides* Herzog nec Spruce, *Syzigiella herzogii* nom. nov. This species is of interest because it has some of the superficial features of *Plagiochila,* while it possesses the restricted rhizoid-initials and plicate, non-compressed perianth of *Syzigiella.* The presence of a *Plagiochila*-like leaf-insertion, of *Plagiochila*-like dentition of the leaves, and of the convex basal fold of the antical leaf-margin (cnemis) all, however, conspire to give the species a distinctive similarity to *Plagiochila.* This similarity is probably owing to a relatively close relationship between the two genera, and is not homoplastic in origin. At any rate, it is certain that *Syzigiella* must be included in the Plagiochilaceae. Müller (1951-54), however, would place it in the Southbyaceae, with which the genus shares the opposite leaves, and the tendency "towards" production of restricted rhizoid-initials.

It should be pointed out that other families (or species within other families) show this combination of subopposite leaves and a restricted rhizoid-initial region found at the underleaf-bases. For instance, some species of *Lophocolea* (*martiana, muricata*), derived presumably from alternate-leaved species of the genus, show this combination of characters. In the genus *Leptoscyphus* of the Plagiochilaceae, many species show a similar combination, as in *Leptoscyphus liebmannianus* (= *Mylia liebmanniana*). Therefore, this combination of characteristics has evolved at least four times, independently, in presumably unrelated groups (Southbyaceae, Lophocoleaceae, as well as in *Syzigiella* and the Plagiochilaceous genera *Plagiochilion* and *Leptoscyphus*). The presence of the combination, since it occurs in both Plagiochilaceae and Southbyaceae, cannot therefore be used to determine the position of the genus *Syzigiella.*

The preceding concepts regarding the position of *Syzigiella* were arrived at before examination of several neotropical species of the genus whose study suggests that *Syzigiella* can be placed unquestionably into the Plagiochilaceae, into the immediate vicinity of *Plagiochila* and *Leptoscyphus.* Although many of the species of the genus, such as *S. plagiochiloides* Spruce (nec *S. plagiochiloides* Herz. = *S. herzogii* Schuster) possess strongly plicate perianths with the mouth contracted, other species, such as *S. perfoliata* (Sw.) Spruce, possess perianths which are midway between those of *Syzigiella* s. str. and *Plagiochila* in facies. The perianths in this latter species are admit-

tedly somewhat plicate distally, and are contracted to the mouth — as in other species of *Syzigiella.* However, they are also clearly laterally compressed, especially above, with the narrowed mouth truncate and somewhat bilabiate; as in *Plagiochila,* the compressed mouth is usually slightly deflexed to the side, at least dorsally. The strong habitual similarity to *Plagiochila* is reinforced by the development of blunt but distinct antical and postical keels. Nearly similar in perianth-form is *Syzigiella purpurea* (Steph.) Schuster, comb. nova (= *Plagiochila purpurea* Steph., Spec. Hep. VI: 194, 1921). In this species the only perianth-bearing plant seen had a bluntly compressed perianth, with the dorsal and postical folds more marked than the lateral weak and rounded plicae, and the moderately laterally compressed distal portion was surmounted by a strongly laterally compressed, narrowed but narrowly and vertically truncate mouth. Although not as plagiochiloid in facies, the perianth of this species nevertheless is clearly transitional from that of *Plagiochila* to that of *Syzigiella.*

This last species, inadequately described by Stephani, is of interest in several other respects. It shows, at least sporadically, terminal branching; it has subrotundate lateral leaves that are narrowly connate postically; there are no underleaves, and the sporadically developed rhizoids are in fascicles from below the point of union of the lateral leaves, with a few isolated rhizoids sometimes inserted somewhat below this point. The purple color, on which the species name is based, of course at once eliminates it from *Plagiochila,* none of whose species are ever purple. Perhaps the most marked feature of the type material are the almost denudate stems: although this may be an artifact, owing to the handling of the dry material; the one male plant seen was not deciduous-leaved. Probably this species produces caducous leaves. If so, the affinity of *Syzigiella* to *Plagiochila,* rather than to the Southbyaceae, is all the more firmly demonstrated.

The species of *Syzigiella* often closely approach *Plagiochila* in other respects. For example, the leaf-shape, the development of marked antical decurrence, and the development of a convex dorsal fold of the leaf in *S. plagiochiloides* Spruce and *S. herzogii* Schuster result in a habitual similarity to *Plagiochila* that cannot be ignored. Inversely, such species as *S. perfoliata* have entire-margined oval leaves, without a dorsal fold, and show no superficial similarity to *Plagiochila*—in spite of possessing a perianth that closely approaches that of *Plagiochila.* (This latter species also deviates from the "normal" species of the genus in not having the rhizoids strictly confined to initial regions; they may be, in part, scattered along the merophytes. Furthermore, *S. perfoliata* shows only a slight union of the bracteole and bracts—unlike typical species of the genus). Such species as *S. perfoliata* exhibit not only unmistakable affinities to *Plagiochila,* but also to the opposite-leaved species of *Leptoscyphus. Syzigiella* differs from both *Leptoscyphus* and *Plagiochila* in a number of significant features: (1) The loss, usually, of underleaves of vegetative stems, with the consequence that the opposite leaves are closely juxtaposed on their postical bases. There is variation here from the

extreme in *S. herzogii* Schuster and *S. appendiculata* Herz. (see Herzog, 1938a, p. 7 and fig. 1a,d) where there is retention of a minute, filiform underleaf, narrowly united on each side with the opposed leaf-bases, to the typical condition in *S. perfoliata* (Sw.) Spruce, where the underleaves are lost, but the juxtaposed postical leaf-bases are hardly united, to the extreme condition in *S. plagiochiloides* Spruce, in which the postical leaf-bases are broadly and conspicuously united. With loss of the underleaves, the rhizoid-initial fascicle comes to be situated at the bases of the leaves, rather than underleaves. (2) The perianth-mouth is narrowed, and at least the distal half of the perianth laterally plicate. (3) The erect and sheathing bracts are variously lobed, united at least at the base with the lanceolate to variously lobed bracteole, the bracts and bracteole together typically forming a lobed and toothed sheath around the perianth-base. In extreme cases the fused bracts and bracteole ("involucrum") form an obconoidal complex that is subtruncate and undulate at the mouth, possessing virtually no indications of an origin from fused bracts and bracteole (*e.g.,* in *S. campanulata* Herz.; see Herzog, 1938a, p. 9, fig. 1e). The frequent tendency towards development of reddish to purplish pigmentation serves to further separate *Syzigiella* from *Plagiochila,* although such pigmentation may also be found in *Leptoscyphus.*

The Genera Mylia Carr. and Leptoscyphus Mitt.—Even though the typical species of *Syzigiella* at first glance diverge strongly from the other Plagiochilaceae, the genus surely exhibits many more marked affinities to the type genus *Plagiochila* than does the genus *Mylia. Mylia* certainly does not "fit" any "better" into the Plagiochilaceae, if the frame of reference for circumscription of that family is derived from the constellation of features shared in common by the taxa exhibiting a clear affinity to *Plagiochila.* Therefore, the writer feels constrained to follow Müller with some hesitation in including the genus in the Plagiochilaceae. Furthermore, as is developed below it is the contention of the author that *Mylia* (as accepted in all recent literature) is merely a form-genus, including three discrete groups that perhaps better deserve to be called genera. These three groups differ widely in the degree of similarity they show to the Plagiochilaceae (s. str.). For instance *Mylia* s. str. (the genus as restricted to include the *M. taylori-anomala* complex) stands alone in the entire family in possessing uniseriate antheridial stalks, and in developing few-celled fasciculate gemmae of the leaf-margins. The second of the segregate genera derived from *Mylia, Leptoscyphus,* exhibits affinities to *Syzigiella* (indicated by the usually restricted rhizoid-initials, and the sub-opposite, often dentate leaves). The third, *Anomylia* (*"Mylia" cuneifolia* and its allies), judging from its mode of vegetative reproduction is more similar to *Plagiochila,* while the restricted rhizoid-initials suggest *Leptoscyphus* and *Syzigiella.*

Even though, on first consideration, *Mylia* s. str. does not appear to fit in the Plagiochilaceae, because of the development of gemmae, a similar diversity

of asexual reproductive modes occurs also in the Lophoziaceae. Here, inversely, we find that fasciculate gemmae are the usual mode of asexual reproduction, while in the sole species, *Acrobolbus rhizophyllus,* we get asexual reproduction by tardily caducous leaves. It should be emphasized that the Lophoziaceae and Plagiochilaceae appear to be the only families where we have such a diversity in asexual reproductive patterns.

Furthermore, other species which have been almost universally placed in *Mylia* (such as *M. cuneifolia* and *antillana*) show asexual reproduction by caducous leaves, as in many species of *Plagiochila.* Since there appears to be little doubt that *Mylia* s. str. (*i.e.,* the gemmiparous species) bears some relationship, even if diffuse, to *Anomylia cuneifolia* and *antillana* (where the present writer would place these species), it appears warranted to include *Mylia,* s. str. in the Plagiochilaceae. At least, we cannot conclude that the mode of asexual reproduction of *Mylia,* s. str., is, *per se,* sufficient reason for excluding that genus from the Plagiochilaceae.

It has been previously emphasized that *Mylia* s. lat. (including *Leptoscyphus*) has been placed in the Jungermanniaceae (Frye and Clark, *loc cit.*; Hara, 1956; Buch, 1936, etc.) or in the Harpanthaceae (Evans, 1940). Although the development of gemmae would, at first glance, suggest that *Mylia* s. str. (excluding *Leptoscyphus*) is not related to the Plagiochilaceae, study of the segregate genus *Leptoscyphus* demonstrated conclusively that it, at least, is closely allied to other Plagiochilaceae. Indeed, it is possible that *Leptoscyphus* is allied more closely to *Syzigiella* than to *Mylia* s. str. Such a hypothesis finds substantiation in these similarities: (1) Primitively both genera, *i.e., Syzigiella* and *Leptoscyphus,* have subopposite leaves that are at least slightly connate at the postical bases with the underleaves. In *Leptoscyphus* large, typically quadridentate or quadrifid underleaves are always retained; in *Syzigiella* the underleaves are reduced to a filiform appendix, usually uniseriate, or are entirely eliminated. (2) In both genera asexual reproduction appears rarely present, and then occurs by means of caducous leaves. (3) The rhizoids typically arise in a fascicle at the underleaf-bases, in both genera, although in each genus there are species where the ventral cortical cells lying below the normal rhizoid-initial region may give rise to some scattered rhizoids. (4) In both genera terminal branching appears to be widespread. (5) Neither genus shows plagiochiloid branching, *i.e.,* positively geotropic flagella are not produced, all the branches being negatively geotropic.

These similarities suggest that the two genera have diverged from a common ancestral type by reduction and eventual obsolescence of the underleaves, associated with retention of a more primitive perianth form (in *Syzigiella*), contrasted to retention — or elaboration — of large and complex underleaves, and development of a laterally compressed, plagiochiloid perianth (in *Leptoscyphus*).

Typical species of *Leptoscyphus* show a distinct union of the large and usually quadridentate or quadrilobed underleaves with the sub-opposed lateral leaves (see, *e.g., Leptoscyphus inflatus* (Herz.) comb. n. = *Mylia inflata* Herzog, *in* Herzog, 1950, p. 56, fig. 8; *Leptoscyphus ligulatus* var. *reflexistipulus* (Herz.) comb. n., = *Mylia ligulata* var. *reflexistipula* Herzog, *in* Herzog, 1954,

p. 38, fig. 5; *Leptoscyphus minutus* (Herz.) comb. n. = *Mylia minuta* Herzog, *in* Herzog, 1955, p. 163, fig. 4h-i; *Leptoscyphus densiretis* (Herz.) comb. n. = *Mylia densiretis* Herzog, *in* Herzog, 1955, p. 200, fig. 27a-3). The existence of species with clearly alternate leaves, with the quadrilobed underleaves free from them (such as *Leptoscyphus hedbergii* (S. Arn.) comb. n. = *Mylia hedbergii* S. Arnell, *in* Arnell, 1956a, p. 547, fig. 14) suggests, as will be brought out in detail later, that the apposition of the leaves and associated union of them and the underleaves are not of great phyletic significance. Nevertheless, subopposed leaves connate with the underleaves are such a common feature of *Leptoscyphus* that I must regard the alternate condition as atypical. Even in *Leptoscyphus hedbergii* some leaves may be subopposite dorsally or postically, as is again emphasized at a later point (p. 26).

Summary.—It should be evident from the above, that the attempt at finding one or several positive characters to set off the Plagiochilaceae appears foredoomed to failure, largely because (unless we restrict the family much more narrowly) the family hardly varies about a single central type, and does not readily admit being defined on the basis of a constellation of characters. Rather, we must conceptualize the family as consisting of a series of divergent evolutionary sequences, some becoming very specialized (*e.g., Tylimanthus*), others retaining patently primitive features (*Syzigiella*) which are linked with the development of very specialized traits. No one genus in the family shows a sufficiently large series of unspecialized features so that it could be postulated to represent an ancestral type.

If we arbitrarily leave *Syzigiella* out of the family Plagiochilaceae, only a single positive character would serve to unite the group, namely, the bilabiate, strongly laterally compressed perianth, wide at the open mouth. Since, as we have seen, *Syzigiella* appears to be more closely allied to the Plagiochilaceae than to the Southbyaceae (or any other family), and since *Syzigiella* typically has a non-compressed, plicate perianth, the natural consequence of its inclusion in the family is the virtual loss of all definite and positive characteristics by which the group could be readily circumscribed. Furthermore, the genus *Cryptocolea* Schuster, which on the basis of oil-bodies would go more nearly into the Plagiochilaceae, but on the basis of its discrete perigynium and absence of underleaves appears allied to *Plectocolea* (in the Jungermaniaceae), also has its reduced perianth laterally compressed and wide at the mouth. Therefore the separation of the Plagiochilaceae from the Jungermanniaceae becomes a matter of some difficulty, accomplished perhaps most readily on the basis of sporophytic characters. (The Jungermanniaceae, except for *Jamesoniella,* have a bistratose capsule-wall; all well-known Plagiochilaceae have it (3-) 4-7 stratose).

It might be postulated that *Syzigiella* serves as a connecting link between the Jungermanniaceae (with terete plicate perianths) and Plagiochilaceae (with bilabiate, laterally compressed perianths), and therefore could be considered a "primitive" genus of Plagiochilaceae. Such a thesis would be difficult to maintain because of the extreme vegetative specialization of the genus *Syzigiella* (opposite leaves,

tending to be united on their postical bases with the rudimentary underleaves or with each other, etc.), which suggest it stands far from the hypothetical ancestral type of the largely alternate-leaved Plagiochilaceae (with their free lateral leaves).

In the final analysis the family Plagiochilaceae is here circumscribed largely on the basis of degree of *affinity* to *Plagiochila,* rather than on the basis of sharp differences from other families. As I have attempted to bring out, there is a complex of genera with rather obvious affinities to each other (*Plagiochila, Chiastocaulon, Plagiochilion, Plagiochilidium, Xenochila*). Allied less closely to these, but nevertheless clearly so, is *Leptoscyphus.* In turn, some species of *Syzigiella,* such as *S. perfoliata,* exhibit marked affinities to both *Leptoscyphus* and the opposite-leaved species placed in *Plagiochilion,* and other species of *Syzigiella,* such as *S. plagiochiloides* and *S. herzogii* possess strong vegetative similarities to *Plagiochila.* Allied, even if not very closely, to *Leptoscyphus* are also the two stenotypic elements, *Mylia* s. str. and *Anomylia;* indeed the affinity of these last three taxa is implied in the previous treatment of them as members of a single genus.

To carry this analysis further, *Pedinophyllum* is closely allied to *Plagiochila.* The controversy regarding the position of *"Plagiochila" lobata* serves to emphasize the immediacy of this relationship.

Finally, *Tylimanthus* cannot be regarded as other than a very specialized derivative of *Plagiochila*-like ancestral types.

It is, therefore, the opinion of the author that the ten generic types cited above show definite interrelationships which are much closer to each other than to genera within other families. In spite of persistent efforts to divorce some of these elements from the Plagiochilaceae (most recently the attempt by Hara (1956) to retain *Mylia* s. str. in the Jungermanniaceae), it is my considered opinion that *if* a family Plagiochilaceae is recognized at all, all of these ten genera must be retained in it.

For orientation of the student I have attempted to contrast the leading characters of these genera in the following synoptic key.

KEY TO WORLD GENERA OF PLAGIOCHILACEAE

This is the first attempt at a key to the genera of the members of the family; like all such initial efforts, it will prove to possess faults. The diagnoses inherent in this key are of necessity somewhat idealized. *Wettsteinia,* sometimes placed in the Plagiochilaceae, but by Müller in the Odontoschismaceae, I have not studied.

1. Asexual reproduction by 1-2-celled gemmae, produced in fasciculate masses from the leaf-margins; leaves entire, rotundate, large-celled (cells 38-50 μ x 45-60 μ or larger in leaf middle); rhizoids of leafy shoots exceptionally dense, forming a mat, extending over the entire ventral merophytes and lateral margins of lateral merophytes; leaves clearly alternate, without a cnemis, free from underleaves; underleaves large, subulate to lanceolate; perianth laterally compressed; antheridial stalk 1-seriate; antheridia 1-2 or 3-5 per bract. .... *Mylia* S. F. Gray, s. str.

1. Asexual reproduction (when present) never by fasciculate, 1-2-celled gemmae; antheridial stalk (where known) 2(-4)-seriate. 2

 2. Plants never developing a perigynium; perianth large at maturity, typically free from and extending beyond bracts; ventral merophytes almost always producing underleaves (these often reduced to 1-2 vestigial cilia); female bracts not margined with slime papillae. 3

  3. Branching normally *via* lateral branches (these may be intercalary, from near the lower base of the leaf-insertion, or may be terminal and of the *Frullania*-type;[2] underleaves distinct, not reduced to a single row of cells;[3] branches never associated with postical, positively geotropic, rudimentary-leaved flagella; rhizoids not restricted to the bases of the lateral leaves (except in *Plagiochilidium*). (Plants never with conspicuous, microphyllous flagella of postical origin.) 4

   4. Leaves clearly and strongly alternate, their postical bases free from the underleaves; perianths strongly laterally compressed, truncated at the mouth. (Never with regularly 4-lobed or dentate underleaves; perianth always typically plagiochiloid.) 5

    5. Rhizoids scattered over the ventral merophytes; leaves very variable, but not obcuneate, rarely simply oblong. 6

     6. Dioecious; leaves "plagiochiloid," *i.e.*, with antical margin more or less deflexed or convolute, forming a cnemis, and with margins usually dentate or lobulate (or both); with a general differentiation into creeping, small-leaved, rhizoidous primary stems and aerial, leafy shoots which lack (or have sparse) rhizoids; usually with some mode of asexual reproduction (caducous teeth or lobes of leaves; caducous leaves; propagula; etc.); entire base of male bracts concave, forming a large antheridial chamber 7

      7. Rhizoids uniformly unicellular; plants not developing multicellular ovoid brood-bodies from the leaf-margins ....*Plagiochila* Dumort.

      7. Rhizoids septate (at least those developed from brood-bodies); leaf-margins of juvenile leaves developing $\pm$ ovoid, parenchymatous, conspicuous brood-bodies, developed singly from the marginal teeth of the leaves. ....*Xenochila* genus nova[4]

     6. Autoecious; leaves flat, rotundate to oblong, entire (rarely shallowly bilobed and/or bearing a few teeth), non-plagiochiloid in facies, without a cnemis; leafy stems creeping, bearing rhizoids; without any mode of asexual reproduction; stem without a differentiated cortex; male bracts with only a small

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[2] In *Anomylia* rarely some postical and intercalary. *Leptoscyphus* often has postical branches; this genus has large, usually quadrifid underleaves.

[3] Except in the monotypic genus *Plagiochilidium* Herz., which is supposedly wholly without underleaves. *Syzigiella* has either vestigial underleaves, connate on each side with the lateral leaves, or lacks underleaves entirely; in the latter case the leaves are slightly to distinctly united in pairs, postically.

[4] See, *e.g.*, Degenkolbe (1938); figs. 84-85, 89-90 and p. 75), who emphasizes that Schiffner believed *Xenochila* might represent a new genus. The genus may be briefly diagnosed as follows: Plagiochilae omnino similis; differt rhizoidibus septatis et gemmis pluricellaribus e marginibus foliorum evolutis. Typus: *Plagiochila paradoxa* Schiffn.

dorsal pocket differentiated as an antheridial chamber .... *Pedinophyllum* Lindb.

5. Rhizoids restricted to a small area at the base of each leaf, or restricted to a small area at the base of each underleaf; leaves either obcuneate or oblong, non-plagiochiloid in facies, without trace of a cnemis, their insertion non-arcuate. 8

8. Rhizoids restricted to a small fascicle at the base of each of the large, lanceolate underleaves; lateral leaves obcuneate, narrowly inserted, almost transverse, freely caducous; leaves and female bracts essentially identical. .... *Anomylia* genus nova (typus: *Mylia cuneifolia*)

8. Rhizoids restricted to a small fascicle at the base of each lateral leaf; underleaves absent; lateral leaves oblong-lingulate, strongly succubously oblique, broadly inserted, persistent; bracts and subinvolucral leaves lobed and dentate on margins .... *Plagiochilidium* Herz. (1931)

4. Leaves usually opposite or subopposite, their postical bases united, on at least one side, usually on both, with the distinct, usually large, underleaves (if without underleaves, the leaf-bases united); lateral leaves entire or bidentate, rarely pluridentate; rhizoids usually restricted to bases of underleaves (rarely extended downward to anterior halves of ventral merophytes); without plagiochiloid branching. 9

9. Perianth laterally strongly compressed, plagiochiloid; underleaves large, usually 4-lobed or dentate; bracts and bracteole not united at base. .... *Leptoscyphus* Mitt. (= *Leioscyphus* Mitt.)

9. Perianth pluriplicate, usually little or not laterally compressed, more or less narrowed to the mouth; rhizoids usually restricted to underleaf-bases (if these are present); underleaves small and unlobed, subulate, or entirely absent; bracts and bracteole united at least at base, often for much of their length. .... *Syzigiella* Spr. (= *Syzygiella*)

3. Branching, in part at least, by means of geniculate *postical* branches of intercalary origin; these develop, at or near their bases (in some or all cases) postical, positively geotropic, descending, reduced-leaved, rhizoidous flagella;[5] plants plagiochiloid in facies; rhizoids restricted to leaf-bases, virtually absent on aerial shoots; underleaves reduced to a short, uniseriate filament. 10

[5] Carl (1931a) first described this distinctive mode of branching, splitting off from *Plagiochila* the genus *Chiastocaulon* on this basis. Hattori (J. Hattori Bot. Lab. No. 3: 34-35, 1948) has shown that *Plagiochila opposita* (R. Bl. et N.) Dumort. has branching approaching this type. He founded the genus *Plagiochilion* for this species, and the closely allied *P. braunianus* Nees. Carl (1931) appears to have quite overlooked the fact that the mode of branching of these two species agreed more closely with that of his *Chiastocaulon* than with *Plagiochila* (in which he retained them).

With study of *Plagiochilion mayebarae* Hattori (Hattori, 1948a, p. 39, fig. 34) this distinction breaks down. This interesting species has postical, endogenous, intercalary branches (much as in the preceding cases). These endogenous branches, in some cases, are positively phototropic, become normally leafy, as in the preceding species. In other cases, these postical branches are, and remain

10. Leaves clearly alternate, narrowly ovate-lingulate; postical, negatively geotropic, leafy branches always bearing, immediately above their base, a postical, positively geotropic, reduced-leaved flagellum; aerial leafy shoots freely branching by means of short terminal branches, of determinate length, of the *Frullania*-type; elaters 1-spiral. ......*Chiastocaulon* Carl

10. Leaves opposite, united slightly postically (below the vestigial underleaves), orbicular to broadly ovate; branches uniformly intercalary, largely or exclusively postical and geniculate; the postical branches very diverse; sometimes some positively geotropic, sometimes all negatively geotropic and giving rise to leafy shoots; the latter type of branch often (sometimes always) giving rise to a postical, intercalary, positively geotropic, stolon-like shoot with reduced leaves and fasciculate rhizoids; elaters (always?) 2-spiral. ....*Plagiochilion* Hattori (= *Noguchia* Hattori; *Plagiochila* subg. *Oppositae* Carl)

2. Plants with perianth reduced or absent; with a discrete perigynium; ventral merophytes *ca.* 2 cells broad, unable to develop underleaves; without any mode of asexual reproduction; rhizoids (where present) scattered; leaves alternate. 11

11. Perianth present, a laterally compressed tube at the apex of the perigynium (which lies in the axis of the shoot); bracts longly exceeding perianth, mussel-shaped, with approximated to appressed margins; branches few, terminal (if present at all) and lateral, except for gynoecial innovations which are always freely produced; without division into prostrate, leafless caudex and aerial leafy shoots, all the shoots similar and leafy; without leafless postical flagella; leaves entire-margined, non-plagiochiloid, without cnemis. ....[*Cryptocolea* Schuster][6]

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flagelliferous, and are negatively phototropic (or positively geotropic). If the branches become leafy and grow away from the substrate, they may remain simple, or they may give rise in turn to a postical branch which is flagelliform and positively geotropic. This flagelliform branch may arise almost at the base of the branch — in which case we have the situation exactly as in *Chiastocaulon,* and as in *Plagiochilion oppositus.* In most cases, however, the flagelliform branch arises some distance above the origin of the leafy branch. In such cases, there is little resemblance to the peculiar condition so diagnostic of *Chiastocaulon.* Two of these variations in mode of postical branching are shown, for *P. mayebarae,* in Hattori (1948a, fig. 34f, g). A study of a portion of the type material (through the courtesy of Dr. Hattori) has shown that, variable as the branching is, *it is uniformly postical.* By contrast, in *Chiastocaulon dendroides,* and in *Plagiochilion oppositus,* lateral leafy branches (in addition to the specialized postical branches) are frequent.

[6] In the absence of sporophytes it is impossible to definitely decide on the position of this genus. For the time being I would place it near *Nardia* in the Jungermanniaceae, from which it differs in the absence of underleaves; the more reduced perianth; the slime-papillae margined, connivent, mussel-shaped perichaetial bracts.

11. Perianth absent, the conspicuous perigynium at right angles to axis, fleshy, rhizoidous; bracts not mussel-shaped and not forming a bilabiate complex; freely branched, the branches frequently lateral (but then axillary and intercalary); branches in part (at least) postical and intercalary, giving rise to leafless postical stolons; with dimorphic shoot-system, the shoots partly rhizoidous and positively geotropic, partly erect and leafy; without subfloral innovations (always?); leaves usually lobed or dentate at apex, plagiochiloid, with cnemis usually distinct. ....*Tylimanthus* Mitt.

I have not included *Apotomanthus* (Spr.) Schiffn. in the preceding key, although Müller (1939-1940) places this genus in the Plagiochilaceae. It possesses a perianth that is trigonous, at least when young, and has a wide, 3-4-lobed mouth. According to Schiffner (1893) it is allied to *Clasmatocolea;* I have not had opportunity to study adequate material of the genus. As already noted, *Wettsteinia* Schiffn. is not included in the key, principally because I have been unable to study material of it. Müller (1951-54) places it in the Odontoschismaceae, although Inoue (1958) places the genus in the Plagiochilaceae.

Comparison of the preceding key shows that of the three subgenera (*Cucullifoliae, Oppositae, Eu-Plagiochilae*) recognized in *Plagiochila* by Carl (1931), the latter two are now considered to represent independent genera, the subgenus *Oppositae* having been elevated to generic standing by Hattori. The third subgenus, *Cucullifoliae,* includes only the single species, *P. cucullifolia* Jack et Steph., ranging from Columbia (Wallis; type!) to Costa Rica. Carl (*loc. cit.,* p. 38) wondered "ob diese merkwürdige Pflanze nicht einem selbstständigen Genus erhoben werden muss . . . " He stated that only study of the perianth could decide this. I have seen several male and female plants, part of the type collection (Farlow Herbarium), and find that the female plants do not show any deviations in the gynoecia. The juvenile perianths are typically plagiochiloid, longly ciliate at the wide and subtruncate mouth; the very immature perianth, as in other species, resembles closely two young bracts, slightly united at base. The leaves of this species are admittedly strongly deflexed and have the entire margins involute, the leaves thus strongly adaxially convex, subglobose or inflated in appearance. However, I am much less impressed with this feature than Carl appears to have been, and do not consider that the strongly adaxially convex, hollowed leaves constitute sufficient basis for a separate genus. They represent a mere extreme extension of the more or less convex leaves that characterize a large number of species in the genus.

It is assumed, in the preceding key, that *Plagiochilidium* Herz. lacks postical branching of the *Chiastocaulon-Plagiochilidium* type. The basis for this assump-

tion is the fact that Herzog (1931) does not call attention to any novelties in branching, and that Carl (1931a, p. 58) who mentions *Plagiochilidium* in connection with *Chiastocaulon,* does not consider that the former is closely allied to *Plagiochila* or *Chiastocaulon,* indeed, considers the *Plagiochila*-like perianth of *Plagiochilidium* as a "Konvergenzbildung." I assume, conversely to Carl's viewpoint, that the *Plagiochila* (and *Chiastocaulon*) type of perianth, together with *Chiastocaulon*-like restriction of rhizoids, points to a distinct phylogenetic connection between *Plagiochilidium* and *Chiastocaulon* (and *Plagiochila*). The assumption of an affinity to *Jamesoniella,* expressed by Herzog in conjunction with the diagnosis of *Plagiochilidium,* appears far-fetched to me.

Carl (1931a) called attention to the fact that *Chiastocaulon* had rhizoids restricted to the leaf-bases, and that this type of rhizoid-restriction "ist ein Merkmal das nach meinen Ehrfahrungen innerhalb der Gattung *Plagiochila* nicht wiederkehren dürfte." Yet, as is evident from the figures in the papers by Hattori (1948, fig. 29E, and 1948a, fig. 34G), and from study of material, the subgenus *Oppositae* of Carl (1931), which he regarded as a member of the genus *Plagiochila,* has exactly this type of restriction of the rhizoids. Admittedly, it is slightly less sharp than one would judge from the figures in Hattori, since at least in *P. mayebarae* Hatt. occasional rhizoids are found on the ventral stem face, below the fascicle present at the "node" where leaves and vestigial underleaf occur in a ring. As a consequence, I conclude that the nature of the restriction of the rhizoids, as well as the mode of branching, place the *Oppositae* in much closer proximity to the genus *Chiastocaulon* than assumed by Carl (1931). Certainly Hattori (1947) was fully justified in raising the *Oppositae* to the rank of a genus, *Plagiochilion. If* one wishes to follow Carl in retaining *Plagiochilion* as a subgenus of *Plagiochila, Chiastocaulon* cannot be given a higher status.

DIAGNOSIS OF THE FAMILY PLAGIOCHILACEAE

The difficulties enumerated above in circumscribing the Plagiochilaceae should adequately clarify and justify the preceding statement *re* the purely temporal value of any attempt at definition of a family Plagiochilaceae. The following diagnosis, therefore, largely serves the negative purpose of eliminating most of the other leafy liverworts, even if it does not serve to sharply define the family.

Plants with *lateral branching of Frullania-type, or intercalary;* with *succubously inserted and oriented,* usually alternate *lateral leaves* (subopposite to opposite in *Syzigiella,* some species of *Leptoscyphus* and *Plagiochilion*); leaves most often entire to subentire, but the *margins often variously dentate to spinose-dentate* (then often with the ancestral bilobate leaf-form indicated by the larger size of two of these marginal teeth), the leaves rarely deeply (to one-half) lobed; dorsal margin often (*Plagiochila,* etc.; *Syzigiella* spp.) reflexed to form a fold or cnemis. *Cells essentially collenchymatous,* rarely becoming equally thick-walled (except for the marginal cells of some species), rarely with trigones virtually absent even under xeric conditions (*Pedino-*

phyllum). *Oil-bodies present,* formed either of discrete, individually protruding globules (then varying, depending on globule size, from finely to coarsely papillose to strongly segmented), or homogeneous and glistening, usually (2) 4-12 (15) per cell, colorless. *Underleaves typically present, but usually small* (ventral merophytes usually 4-6, rarely only 2, rarely 7-8 cells wide; the underleaf-width thus usually 3-6 cells at base), reduced to stalked slime papillae in some species, rarely larger and almost leaf-like, most often free (but united with postical bases of adjacent leaves in *Syzigiella* and *Plagiochilion;* in the latter genus with underleaves often vestigial, then with postical leaf-bases juxtaposed or even briefly connate). Branching variable: usually "axillary," and intercalary from the postical half of the leaf-axil [*fide* Müller (1905-1916, p. 775) from the upper part of the line of insertion of the leaves in *Pedinophyllum;* I have not been able to find axillary branching from the upper half of the axil in this genus], but sometimes of the *Frullania*-type (and terminal); often with development of a primary leafless rhizogenous system of primary stems and leafy, rhizoid-free aerial stems (*Plagiochila*) or with ventral stolons (*Plagiochilion*). Rhizoids occurring scattered over the postical merophytes (*Plagiochila, Mylia* s. str., *Pedinophyllum*), or restricted to the bases of the underleaves of leafy shoots (*Anomylia, Syzigiella,* most species of *Leptoscyphus*) or occurring largely restricted to ring-like nodes (homologous to leaf and the underleaf-bases) of small-leaved ventral flagella (*Plagiochilion*). *Asexual reproduction variable,* rarely (*Mylia,* s. str.) by fasciculate 2-celled gemmae; more often by caducous leaves (*Plagiochila* spp., *Anomylia*), or by caducous teeth or lobes or fragments of the leaves (*Plagiochila* spp.); often with development of leafy propagula from cells of the leaf-surface (*Plagiochila*); in other cases (*Leptoscyphus* spp., *Pedinophyllum*) with no asexual mode of reproduction.

Usually dioecious (*Pedinophyllum* monoecious). *Position of sex organs unspecialized. Perianths terminal* (absent in *Tylimanthus!*), apical on leading shoots or on leafy branches, often with 1 or 2 subfloral innovations, *wide at the mouth and normally strongly laterally compressed* (terete and ± plicate only in *Syzigiella*), *thus bilabiate. Perigynium at base of perianth absent* (except in *Tylimanthus* and in *Cryptocolea,* which perhaps belongs in Jungermanniaceae). Androecia terminal on elongate, leading or lateral branches or main stems, often *becoming intercalary,* rarely on short lateral intercalary branches, of usually 4-12 pairs of bracts (thus *distinctly spicate*); androecial bracts somewhat smaller than lateral leaves usually, with one antheridium each (*Pedinophyllum*) or 1-2 or more (*Plagiochila, Mylia,* etc.); paraphyses absent in perigonal bracts. Antheridia large, subglobose to broadly ovoid, to *ca.* 320-350 μ wide x 340-375 μ long, the wall of numerous, irregularly oriented cells; stalk moderately long (> 150-310 μ), *of (1) 2-4 cell rows.* [Müller (1951-54: fig. 16) figures and describes the antheridial stalk of *Plagiochila asplenioides* as biseriate. As with almost all other cases studied, there is considerable variation

in this respect. In *P. echinata* Schuster, for instance, the antheridial stalks are fundamentally biseriate, but occasional or many of the cells undergo a supplementary vertical division, resulting in a locally 3-4-seriate stalk. As far as known only *Mylia* s. str. *has a uniseriate antheridial stalk.*] Sporophytes with *seta of numerous rows of cells; capsule ovoid or short-ellipsoid,* 4-valved to base; valves elliptical, straight, *normally* 4-7 *stratose.* Inner layer (in all examined groups) with tangential, band-like thickenings; outer with radial, nodular thickenings. Spore-elater diameter ratio varying from 2:1 to 1.3:1. Elaters free, bispiral, rarely in part trispiral (in *Chiastocaulon* unispiral).

The above diagnosis is ambiguous in several respects, for reasons to be discussed in the following section. In one respect, in particular, do we find an unusual degree of variability of the family: the occurrence, and restriction of the rhizoids. It is my opinion that rhizoids restricted to the bases of the leaves is a primitive feature throughout the Jungermanniales, while dispersed rhizoids are associated usually with derivative groups. The little work done with the ontogeny of the group would appear to bear out this supposition. In *Mylia anomala* the developing sporelings, for example, undergo a juvenile stage where the leaves are isophyllous (*i.e.,* where no differentiation in size between leaves and underleaves occurs). During that stage, rhizoids are found only at the bases of the underleaves. It is only later that rhizoids develop elsewhere on the ventral merophytes, and from the portions of the lateral merophytes below the postical leaf-bases.

In *"Mylia" cuneifolia* (*Anomylia cuneifolia*) a reduced species, even the mature plant shows such a restriction of rhizoids of the underleaf bases, with rare development of one or two rhizoids from the homologous position at the bases of the lateral leaves.

Indeed, there is a tendency throughout the family for restriction of rhizoids to the bases of the underleaves (and/or lateral leaves). In most cases they occur only at the underleaf bases, but in some genera (*Plagiochilidium* Herzog, *Plagiochilion* Hattori) they are confined or nearly confined to the postical bases of the leaves. In *Plagiochilidium,* indeed, there is a distinct tuft at the postical base of each leaf (the underleaves being wholly lacking, according to Herzog, 1931, p. 187, fig. 1). *Plagiochilion,* which differs from *Plagiochilidium, e.g.,* in the opposite leaves, agrees in the absence of underleaves, or their obsolescence, and in that the rhizoids are restricted largely to the bases of the leaves (often, on flagella, to the bases of highly reduced leaves, then appearing to occur in "nodes" or "rings" around the flagella), but a few may occur on the merophytes some distance behind the "nodes."

In *Syzigiella* there is a similar restriction of the rhizoids: this time to the bases of the minute underleaves that are connate at bases with the opposed leaves, or (with loss of the underleaves) to the area immediately below the point of union, ventrally, of the leaves.

In *Mylia,* s. str., the majority of rhizoids, and often almost all of them, occur in tufts at the bases of the leaves and underleaves, although scattered ones are found elsewhere on the ventral portion of the axis. As is brought out under the discussion of *Mylia,* the allied genus *Leptoscyphus,* with largely opposed or sub-opposed leaves, tends to have the rhizoids more restricted, to the bases of the underleaves, or at least to the underleaf-bases and the portions of the ventral merophytes situated immediately posterior to them. Indeed, there appears to be a correlation in the family between a tendency for the opposition of leaves, a derivative character, and the restriction of the rhizoids to the underleaf-bases (or, if the latter become obsolete, to the leaf-bases). The latter, in spite of this, appears to be a primitive character, judging from ontogeny. It is only in the *Plagiochila* and its immediate allies (*Chiastocaulon, Pedinophyllum*) that we have a development of a wholly unrestricted dispersal of the rhizoids along the postical face of the axis. In these genera there is no tendency at all for the leaves to be opposed.

RELATIONSHIPS OF THE FAMILY

IS THE FAMILY MONOPHYLETIC?

As is evident from the preceding discussion, almost the sole positive character binding together the genera here placed in the Plagiochilaceae is the laterally compressed, bilabiate perianth. Furthermore, in this respect most species of *Syzigiella* represent an exception to the rule while *Tylimanthus* has lost the perianth. Other primary characteristics (succubous leaf-insertion; discrete but small underleaves; primarily or exclusively lateral branching; intercalary androecia; presence of several oil-bodies in all cells; generally collenchymatous cells; lack of, or shallow bilobing of, the leaves; unspecialized [terminal] position of gynoecia on elongate shoots; pluristratose capsule wall) are not sufficiently diagnostic, singly or in combination, to sharply define the group.

This suggests that perhaps the utilization of a laterally compressed, widely truncate perianth-mouth as a family character is unwarranted. It is obviously quite possible that there has been evolution two or more times of a laterally compressed perianth, from a terete ancestral prototype—in which case the family, as now constituted, becomes polyphyletic. This viewpoint is implied, at least, in the classifications employed by Evans (1940) and Buch (1936), in which the Plagiochilaceae are restricted to *Plagiochila* (or to this and immediately related types), with Buch going so far as to include *Pedinophyllum,* as well as *Mylia* in the Jungermanniaceae. The problem of the relationships of the Jungermanniaceae and Plagiochilaceae, therefore, deserves further study (see the immediately following section).

In the opinion of the writer, it probably would be well to follow largely the concepts of Müller (1951, p. 197) as regards delimitation of the family, for the following largely negative circumstantial reasons:

(1) *Pedinophyllum* is distinctly related to *Plagiochila,* as regards capsule-wall, rhizoid distribution, underleaf size, the tendency to produce shallowly bilobed and occasionally few-dentate leaves; see p. 60. (2) *Mylia* appears to show at least a distant relationship to the entire-leaved species of *Plagiochila,* and is certainly allied to *Anomylia;* the latter shares a similar asexual reproductive mode with many species of *Plagiochila;* however, the development of caducous leaves in both *Anomylia* and *Plagiochila* may represent a homoplastic development correlated with epiphytic occurrence vs. the terrestrial occurrence of the non-caducous leaved types. Similar reproductive modes have developed independently in other groups (Radulaceae, Frullaniaceae, Lejeuneaceae) that have become largely arboreal, as well as in isolated species in families that usually do not show caducous leaves, *i.e., Bazzania,* some species of *Herberta. Mylia* agrees in the polystratose capsule wall with *Plagiochila.* (3) These three genera are related at least as clearly to *Plagiochila* as to any generic group in the Jungermanniaceae. The writer would furthermore follow Carl in placing *Syzigiella* in the vicinity of *Plagiochila*—a relationship also implied by Herzog (1932b); the position of that genus in the Southbyaceae (as in Müller, 1951, p. 197) appears much less natural, as has already been developed.

The close relationship of the segregate genera *Plagiochilion, Plagiochilidium,* and *Chiastocaulon* to *Plagiochila* is acknowledged by all students of the group; therefore, these genera do not enter into the problem of circumscribing the family, and hence are not further discussed here.

Finally, as a completely aberrant element in the family, we must consider *Cryptocolea* Schuster (see Schuster, 1953). This monotypic genus was at first considered to represent a subgenus of *Plectocolea* (Jungermanniaceae), to which it is allied in the presence of a perigynium, in the absence of underleaves, scattered rhizoids, and the nearly orbicular leaf-form. However, the wide-mouthed, somewhat laterally compressed perianth, and the exceedingly distinctive oil-bodies are quite unlike *Plectocolea.* Furthermore, the perianth is hidden between the mesally connivent and approximated apices and margins of the perichaetial bracts (which simulate a dorsally keeled, plagiochiloid perianth). These latter bear at their apices a border of slime papillae — characters which do not occur again in either *Plectocolea* — nor in any plagiochiloid genus. The vegetative plant, with an appearance much like a small *Mylia* or a *Plectocolea* (the androecia also exhibit definite affinities to both of these groups) does not give us a clue as to its disposition. At present, *Cryptocolea* is considered a highly derivative element in the Jungermanniaceae, in spite of the wide-mouthed, laterally compressed perianth, and the segmented oil-bodies. Study of the mature capsule may demonstrate the genus should be considered a derivative element in the Jungermanniaceae. The chief reasons for removing *Cryptocolea* from the Plagiochilaceae to the Jungemanniaceae (presence of perigynium; absence of underleaves) would apply equally to eliminate *Tylimanthus* from the Plagiochilaceae. Yet the facies of the latter is indubitably plagiochiloid! For the time being, therefore, the position of *Cryptocolea* must remain in question.

RELATIONSHIPS WITH OTHER FAMILIES

The Plagiochilaceae, as restricted here, exhibit at least superficial similarities to the Jungermanniaceae, and (through *Syzigiella*) may also be related to the Southbyaceae. Certain genera (*Leptoscyphus*) also exhibit at least a superficial similarity to the Southbyaceae and some Lophocoleaceae. The differences between the Plagiochilaceae and these three families therefore deserve emphasis—in so far as we can suggest definitive differences. Affinities to other families of Hepaticae do not exist.

From the preceding section, it is obvious that there has been, in recent years, considerable differences of opinion as to the limits between the Jungermanniaceae and Plagiochilaceae. Both families have gynoecia and androecia in "unspecialized" positions. Such genera as *Pedinophyllum, Mylia* (s. lat. = *Mylia, Anomylia, Leptoscyphus*), and *Cryptocolea* could be placed with some justification into either of these families. However, in the present work the first two, of these three, complexes are placed in the Plagiochilaceae for two reasons: (1) They have a laterally compressed perianth vs. a terete, uncompressed one in all "true" Jungermanniaceae—a definite phyletic advance. (2) They retain a relatively thick capsule-wall, vs. the reduced, bistratose capsule-wall of all Jungermanniaceae excepting only *Jamesoniella;* in this, the Plagiochilaceae are more "primitive." These two characteristics, in the final analysis, represent the major ones distinguishing these two families. Furthermore, in the Plagiochilaceae we have, normally, either glistening homogeneous oil-bodies, which (in most cases) are divided into few to numerous protruding segments or globules; only in the *Mylia taylori-verrucosa* complex do we find oil-bodies formed of an infinite number of minute, non-protruding spherules. By contrast, the Jungermanniaceae appear to possess, in all European, North American and Japanese species studied, oil-bodies formed of numerous minute, essentially non-protruding spherules (which may be so difficult to perceive that the oil-body is virtually homogeneous in appearance); only in *Nardia* and a few species of *Solenostoma* do we find virtually homogeneous oil-bodies—but in no case do segmented oil-bodies occur. To what degree the predominantly segmented form of the oil-bodies of the Plagiochilaceae will serve to separate that family from the predominantly non-segmented oil-bodies of the Jungermanniaceae must remain an open question until all genera and more species of some of the larger genera are studied. None of the Jungermanniaceae ever show a restriction of the rhizoids, a feature common in the Plagiochilaceae.

Although a remote connection with the Jungermanniaceae is postulated here, the Plagiochilaceae appear to have evolved in a different direction. We find the first family shows early reduction of the capsule-wall to the bistratose condition, and early reduction of the underleaves, while retaining such features as a plicate non-compressed perianth, a higher (2:1) spore-elater diameter ratio, etc. The Plagio-

chilaceae, on the other hand, retain a 4-8-stratose capsule-wall, and retain distinct underleaves in almost all cases, while exhibiting in all genera (except *Syzigiella*) a marked compression of the perianth, and often although not uniformly a reduced (1.5-1.3:1) spore-elater ratio. The first family also shows, early in its development, a marked tendency for the development of a perigynium; in the Plagiochilaceae no perigynium develops (except for *Tylimanthus*), unless *Cryptocolea* is included (a genus perhaps better regarded as a highly modified member of the Jungermanniaceae; it differs from our other genera in the total lack of underleaves, and in the distinct perigynium).

The relationships of the Plagiochilaceae to the Southbyaceae are diffuse at best, only the genus *Syzigiella* suggesting a close affinity. The Plagiochilaceae, except for some species of *Syzigiella,* have a laterally compressed perianth; in the Southbyaceae, the perianth is reduced or absent, and when present merely a short tube above the extensive perigynium. The Southbyaceae have a 2-stratose capsule-wall, like the Jungermanniaceae; in this character the family departs from "normal" Plagiochilaceae. It would be possible, however, to consider the Southbyaceae as derived from near *Syzigiella*—which is more primitive than that family, because of the absence of a discrete perigynium. As previously developed, the moderately laterally compressed perianth of various species of *Syzigiella* is definitely suggestive.

The relationships to the Lophocoleaceae appear to be somewhat less remote. The similarities in leaf-form, restriction of rhizoid-initials, and union of the subopposite leaves with the underleaves, of such groups as the *Leptoscyphus repens* group, and of the *Lophocolea martiana* group, are possibly the consequence of parallelism in development (as has been previously mentioned). The trigonous perianth of the Lophocoleaceae, with a sharp keel on each side, suggests a fundamentally different group, at first glance.

However, certain similarities between the Lophocoleaceae and Plagiochilaceae suggest a rather distinct relationship: among them the sharp tendency in both groups to have bilobed or bidentate leaves able to produce supplementary teeth (compare *Plagiochila* with *Lophocolea heterophylla* and *Chiloscyphus*); the retention of a 4-several stratose capsule wall; the tendency towards a low spore-elater diameter ratio (usually *ca.* 1.7-1.3:1 in Plagiochilaceae; usually 2-1.7:1 in *Lophocolea,* but down to 1:1 in some species, such as *L. heterophylla* and *minor*); the usual occurrence of segmented or coarsely papillose oil-bodies, rather numerous per cell; the tendency towards restriction of rhizoid-initials to underleaf-bases (which is more rigidly fixed in the Lophocoleaceae, however); the tendency to develop subopposite leaves which fuse at their bases with the underleaves; the retention of small but relatively discrete underleaves, i.e., lack of obsolescence of the ventral merophytes; the terminal position of the gynoecia; general lack of any tendency to produce a perigynium (except in the doubtfully placed *Cryptocolea*); the wide and open mouth of the perianth. The

many similarities, and evolutionary tendencies that recur in both families suggest a common ancestry.

A possible relationship of the Plagiochilaceae to the Lophocoleaceae is also indicated by such species as ***Leptoscyphus hedbergii*** (S. Arn.) comb. n. (= ***Mylia hedbergii*** S. Arnell, Arkiv för Bot. Ser. 2, 3(16):547, fig. 14, 1956a). This species, unlike the majority of species of ***Leptoscyphus*** has rather obviously alternate leaves, although here and there the leaves may be subopposite at their postical bases or at their antical bases, or both; the underleaves, which are bifid with 1-2 (3) lateral, ciliiform teeth, are characteristically and longly decurrent (much more so than shown by Arnell), although the decurrent strip becomes vestigial before intercepting a leaf-base, hence the underleaves are free or only exceptionally slightly united on one side with an occasional leaf-base; the rhizoids are confined to initial-areas at the summit of the inverse U-shaped underleaf-insertions. These features are all such as recur again with some regularity in many species of ***Lophocolea***. The single perianth which I have seen (in ***Hedberg*** 620!) reinforces the similarity to ***Lophocolea***. It is wide at the mouth, and trilabiate rather than bilabiate, the two lateral "lips" being admittedly much broader than the postical "lip," which is also shorter. It is thus evident that, much as in ***Plagiochila tricarinata*** Carl, the ventral merophytes may contribute to the formation of the perianth. In essence, then, one can postulate an origin of the Plagiochilaceae from Lophocoleaceae-like ancestral types by a gradual process of reduction of the ventral merophytes, associated with which the perianths become bilabiate rather than trilabiate. As is well known, both families possess perianths that are typically very wide at the mouth. The occasional difficulty in separating species of ***Leptoscyphus*** from ***Lophocolea*** is well known; it has led, ***e.g.***, to the description of African forms of ***Lophocolea cuspidata*** as "***Leptoscyphus stephensii***" by Sim, and the similar description of plants of ***Lophocolea newtoni*** as "***Leptoscyphus leightonii***" by Sim.

In summary, remote relationships between the Plagiochilaceae and the Southbyaceae and Jungermanniaceae are postulated, but the probability of a much more immediate affinity to the Lophocoleaceae is admitted. Specifically, it is pointed out that both families are nearly unique in the wide-mouthed perianth. The presence of a distinct, if narrow, ventral, third "face" of the perianth in some species (***e.g.*** in ***Leptoscyphus*** and ***Plagiochila***) suggests the Plagiochilaceae have been derived from Lophocoleaceae by (1) gradual narrowing of ventral merophytes, associated with, (2) narrowing of the contribution of ventral merophyte to perianth, and eventual loss of any such contribution; (3) reduction of the underleaves; and, (4) development of a scattered rhizoid dispersal pattern. The widespread occurrence of both intercalary, axillary branches and lateral, ***Frullania***-type branches, in both families, is suggestive. So is the rarity of reproduction by gemmae, and the general inability to develop a perigynium.

TECHNIQUES AND MATERIALS STUDIED

The accuracy of identification of the Plagiochilaceae, especially of the species of *Plagiochila,* depends to a large degree on accuracy of measurements. Since the measurements of leaf-form, and of cells within the leaf, tend to be subjectively conceived, the following outline of the procedure used by the author is given, in order that his measurements shall be strictly subject to duplication.

1. *Cell size.*—The size of the cells is measured by averaging that of a linear series of cells (3-6, depending on size) and measuring them with

the ocular micrometer as a series. Several measurements are made; the upper and lower figures given represent the averages of several measurements of series of cells (divided, of course, by the number of cells involved). Since up to a 75 percent variation, both in cell width and length is to be expected with individual cells, it is obvious that measurements of isolated cells can have little meaning. The cells are measured at the following points (indicated in Fig. 1, A):

a. *Cells of leaf-apex,* within the 1-2 rows of sometimes modified marginal cells.
b. *Cells of leaf-margin* (measured *ca.* ½ of the distance from apex to base, on stretches of the postical margin not interrupted by teeth); the width of these cells is determined by making isolated measurements of the marginal row and averaging them.
c. *Median cells,* measured strictly midway between base and apex of leaf, along or near the midline of the leaf.
d. *Basal cells,* measured in the basal 1/10 of the leaf, at or near the midline of the leaf.
e. *Cells of postical base.*

2. *Leaf-dimensions.*—It is important, for the correct interpretation of leaf-form, to study mature leaves of main stems of the more (or most) robust plants available. It should be remembered that juvenile plants and plants from abnormal sites often are so modified that their leaf-form (and dentition) are scarcely typical of the species; such plants sometimes prove unrecognizable, until the student becomes thoroughly familiar with the entire variation-pattern of the several species.

a. *Leaf-width.*—This is measured at the widest point, ***above*** the decurrent strip; in the case of ovate-leaved plants, just above the decurrent bases; in the case of obovate forms, above the leaf middle.

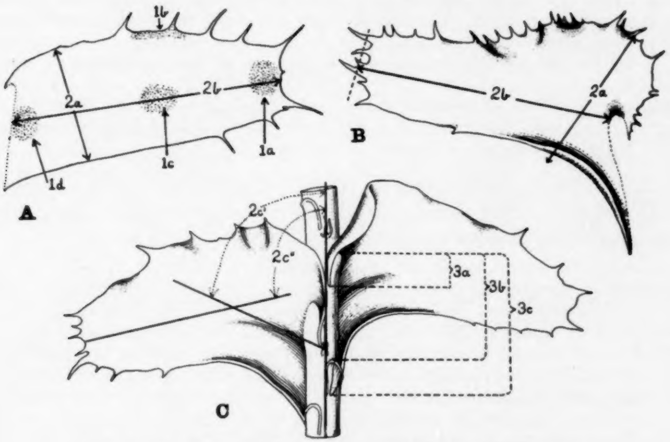

Fig. 1.—Leaf proportions and insertion angles (see text).

b. *Leaf-length.*—This is measured along an imaginary midline, and extends to an imaginary line cutting off the apices of the longer distal teeth.
c. *Leaf-angle.*—This is also measured, using as one side of the angle the imaginary midline of the leaf, as the other side, the vertical line formed by the stem.

It must be noted that measurements of the leaves should be made from leaves dissected free, and flattened under the cover glass, and not from leaves *in situ* on the stem. Furthermore, all measurements should be made from leaves of mature form, from robust (and presumably mature) plants. With abnormal growth conditions plants may retain a persistently juvenile form, and the leaf dimensions and shapes may then depart considerably from the norm. Also, on branches the leaf sizes and dimensions are usually considerably different than on main axes.

The angle at which the leaf spreads from the stem involves two components. One consists of a variable degree of postical displacement from the stem, the leaves tending to be somewhat secund (in *Plagiochila*); this cannot be readily measured, and is best evident from lateral views of the plant(see e.g., the figures of *P. sharpii*). The second component consists of divergence from the shoot apex. In the case of non-falcate leaves, this is measured simply by taking the angle (2c′ in Fig. 1) formed between an imaginary midline through the leaf, and the midline through the axis. In many cases the leaves are somewhat falcate, and the angle of divergence, or "spreading" increases from an angle 2c′ to 2c″ (Fig. 1).

3. *Decurrence and length of line of insertion.*

a. Decurrence of the postical base: This is measured from the highest point of leaf-insertion of the postical base, the point at which the decurrent strip merges into stem-tissue (Fig. 1, 3a). It is expressed as a fraction of the length of the lateral merophyte (equivalent in length to the distance 3*b* in Fig. 1).
b. Length of line of insertion: Measured (on leaves carefully dissected off, so that dorsal insertion is intact) from highest point of line of insertion, to the greatest point of dorsal decurrence (Fig. 1, 3c).

4. *Leaf form.*—The leaf-form is determined from leaves dissected from the main stem, and flattened under the cover-glass. Four basic leaf-forms are found in our species:

a. *Orbicular and suborbicular* (*P. asplenioides*, forms).
b. *Ovate* (varying from broadly ovate, when less than 1.5 as long as wide, to narrowly ovate, when 1.5-2.5 as long as wide). The leaves are virtually never symmetrically ovate, therefore, in the descriptions that follow no attempt is made to distinguish between symmetrically and asymmetrically ovate: all our species have leaves of the latter type. In many cases, the ovate nature of the leaf is partially modified by the long decurrence of the antical base, and the attenuation of the apex, resulting in an ovate-oblong and somewhat falcate leaf form. (Fig. 1, B-C.)

c. *Lingulate to narrowly rectangular* (varying from 2.0-3.0 times as long as wide, with the postical margin scarcely arched and nearly parallel to the antical; the leaf is never dilated above the postical base and is widest near the middle, if at all with a clearly determinable wide point). (Fig. 1A.)

d. *Obovate.*—With the maximum width a little to considerably above the leaf-middle, and the postical base never dilated at all; the length less than 1.9 the leaf-width.

Types *a* and *b* intergrade, and correspond in leaf-insertion roughly to the "Ampliatae" of Stephani; types *c* and *d* also intergrade, and correspond nearly to the "Patulae" of Stephani.

It should be noted that leaf-shape is determined by ignoring the marginal teeth of the leaves.

Materials studied.—This monograph is based to a large extent on personally collected materials. The rich collections in the New York Botanical Garden have been studied (NYBG), as well as the extensive collections of the University of Tennessee Herbarium (UT), and the equally extensive collections at Duke University (DU) and at Yale University (YU). In addition, individuals of the materials at the University of Minnesota (UM), and in the collection of Paul M. Patterson, Hollins College (PMP) have been examined. For study of the relevant elements in the east Asiatic flora, I have depended largely on the exsiccatae, Hepaticae Japonicae (Hep. Jap.), issued by Dr. Sinske Hattori; for study of the neotropical flora, I have depended largely on collections received from Dr. Th. Herzog, and on the collections at the New York Botanical Garden. It should be noted that throughout this work the chief emphasis has been on the living plant, and such aspects best studied from fresh material as mode of asexual reproduction, type of oil-body, ecological restrictions and micro-distribution, etc. For that reason, the largest emphasis has been on personally collected materials.

For the aid of future workers in the group, illustrations have been prepared almost exclusively from personally collected plants in my herbarium. All packets from which illustrations and slides have been prepared have been labelled to that effect. For further reference for future critical work, I have indicated on the plate legends the collection number of the specimen from which the individual figures are derived.

It has not been considered worth the extra space it would entail to cite the repository of individual specimens studied, since the majority of cited material is in the writer's collection, the remainder in the relatively few sources cited above. Duplicates of much of the writer's material are available at The Naturhistoriska Riksmuseum, Stockholm, Sweden; the herbarium of Duke University; the herbarium of the Hattori Botanical Laboratory. A considerable number of specimens have been widely disseminated through the exchange maintained by the American Bryological Society.

I have made it a practice to cite (usually accompanied by an exclamation mark!) all collections studied, except that those personally made are not marked with an exclamation mark. Only in very common species, such as *Mylia anomala* and *Plagiochila asplenioides* have I limited myself to citation of representative collections. Actual collections seen have the collector's name set in italics (in the absence of a collection number, year of collection is cited); the scattered literature reports I have considered to be authentic have the authority, and year of the citation, indicated, but these are set in roman letters.

KEY TO NEARCTIC GENERA OF PLAGIOCHILACEAE

1. Cells small or moderate in size: the median 16-36 (40) μ wide; leafy shoots with rhizoids absent or usually sparingly developed; asexual reproduction absent, or via caducous leaves, leaf-lobes or teeth, or by propagula formed individually from leaf cells; antheridial stalk usually 2-seriate. 2
    2. Rhizoids, where present, scattered over the postical face of stem; leaves various in shape, inserted by a broad line (at least half the width of the leaf), never obdeltoid; plants small to very robust, never minute; frequently with sex organs present; underleaves usually minute or very small; cortical cells in numerous rows, never larger than medullary in diameter 3
        3. Dioecious and often sterile; usually with ascending to erect shoots; leaves with dorsal margin ± postically deflexed or revolute, at least near base (forming a cnemis, or convex fold, which is most conspicuous in drying), variously dentate or lobed, only rarely entire or subentire; usually with some mode of asexual reproduction; cells usually with discrete, often large to bulging, trigones; oil-bodies small, homogeneous to coarsely segmented, rarely granular-segmented; male bracts with entire basal portion inflated to form an antheridial chamber, the bracts usually closely imbricate and forming a compact spike; stem with a distinctly differentiated cortex of ± tangentially flattened, thick-walled cells, smaller in diameter than medullary cells, usually 2-3 (4-5) cell-layers thick, never mycorrhizal; rhizoids of leafy shoots usually rare or lacking. ....*Plagiochila* Dumort.
        3. Autoecious, usually fertile, and without any mode of asexual reproduction; shoots all prostrate, none rhizomatous; leaves with dorsal margin nearly or quite flat, without a cnemis, rounded at apex (rarely shallowly bilobed; without spinose marginal teeth); cells with trigones minute; oil-bodies very large, nearly filling cell-lumen, finely granulose and opaque in appearance; male bracts with only the dorsal portion of base pocket-like, monandrous, the bracts lax, the spike loose; stem with cortex hardly differentiated, the cortical cells hardly flattened, nearly equal to medullary in diameter, often mycorrhizal; leafy shoots with abundant rhizoids. ....*Pedinophyllum* Lindb.
    2. Rhizoids few, restricted to a small fascicle at the bases of the large, ovate to lanceolate underleaves (rarely a few also at postical bases of leaves); leaves obdeltoid to obovate-obdeltoid, inserted by a narrow line, almost transversely oriented, freely caducous; plants minute; habitually sterile; stem with cortical cells in few (8-12) rows, averaging slightly larger in diameter than medullary, not thicker-walled, not mycorrhizal. ....*Anomylia* genus nova
1. Cells very large, the median (38) 40-50 μ wide, with coarse trigones; leafy shoots with dense rhizoids, forming a thick mat in which the entire, lanceolate to subulate underleaves are hidden; asexual reproduction *via* fasciculate, 1-2-celled gemmae from the apices of the leaves; leaves subrotund, without a cnemis, the antical margin incurved or flat; cortical cells numerous, not differentiated from medullary (in cross-section), thin-walled, at least externally; antheridial stalk 1-seriate. ....*Mylia* S. F. Gray

MYLIA S. F. Gray, emend. Carr.

Mylia S. F. Gray, Nat. Arr. Brit. Pl. 1:693, 1821 (as *Mylius*); Carrington, Trans. Bot. Soc. Edinburgh 10:305, 1870.

The nomenclatorial history of this genus is complex. The generic

synonymy is so diverse (*Leptoscyphus, Leioscyphus, Mylius, Coleochila, Clasmatocolea*) that some analysis of the present usage of the name seems necessary before any attempt is made at a diagnosis.

The oldest of these names is *Mylius* S. F. Gray (Nat. Arrang. Brit. Pl. 1:693, 1821); this was based on four species of *Jungermannia*, listed in the following order: 1. *taylori*, 2. *anomalus*, 3. *polyanthus*, 4. *cuneifolius*. The writer would suggest that the first species, *M. taylori*, be considered the genotype, in which case the second species (*M. anomalus*) is clearly congeneric with it. The third species is today placed in the genus *Chiloscyphus*, so need not further concern us. In the writer's opinion, developed subsequently, the fourth species (*M. cuneifolius*), though today almost universally placed in this genus, cannot be maintained in *Mylia*.

The next generic name, *Leptoscyphus* Mitten (London J. Bot. 3:358, 1851) was based on *Jungermannia liebmanniana* Lindenberg, a species (judging from the material distributed from the Andes, in the *Hepaticae Spruceana*) that possesses bifid underleaves to whose bases the rhizoids are confined, with small cells (35 μ or less in the leaf middle; with large brownish trigones), and with nearly approximated subopposite leaves. This species, though approaching *M. taylori* in robustness, differs in certain important respects (particularly the absence of gemmae) from *Mylia*, s. str., and should not be considered congeneric with it. Mitten (*loc. cit.*) cites, among others, the following species for this genus: *L. succulentus, taylori, pallens, aequatus, turgescens, strongylophyllus, chamissonis, nigricans, gibbosus* . . . "and probably *L. cuneifolius*." The present writer would not regard *L. taylori* and *L. cuneifolius* as congeneric with *Leptoscyphus* s. str.

Some 23 years later, Dumortier (Hep. Eur. 105, 1874) founded the genus *Coleochila* with *J. taylori* as the first species cited. The writer would suggest this be regarded as the genotype, upon which the genus may be allowed to disappear as a later synonym of *Mylius* Gray (= *Mylia* Gray, emend. Carr.).

Spruce (Trans. Bot. Soc. Edinburgh 15:440, 1885) described the genus *Clasmatocolea*, with the first species cited *C. fragillima*. The writer would suggest that following the reasoning of Grolle (1956), *C. exigua* be regarded as the genotype. Spruce states (*loc. cit.*) that "I cannot doubt that the Irish *Jung. cuneifolia* . . . is a true *Clasmatocolea*," and stresses its similarities to *C. fragillima*. Although, with this, Spruce clearly indicated his belief that *J. cuneifolia* was not to be regarded as a *Mylia* (with which the writer would agree), the disposition in *Clasmatocolea* does not appear to be particularly fortunate. I have not been able to study the genotype of the latter genus, but on the basis of the study of Grolle (1956), and a detailed study of *C. doellingeri* (living material, leg. Schuster, from Juniper Springs, Fla.) which is regarded as representing a second genus (*Chonecolea*) by Grolle, I cannot conclude that *J. cuneifolia* can be placed in *Clasmatocolea*, however this genus is restricted. Among the important

cytological differences are the thin-walled, non-collenchymatous cells, with many minute and almost homogeneous oil-bodies of *Chonecolea* (and presumably *Clasmatocolea*) vs. the strongly collenchymatous cells with few, large, coarsely papillose oil-bodies of *J. cuneifolia.* Furthermore, all true species of *Clasmatocolea* possess a tetragonous perianth, somewhat tetragonous-campanulate in form. As Evans (1923, p. 56) has pointed out, *Mylia antillana* Carr. & Spruce, from the West Indies, which is very close to *M. cuneifolia,* has a strongly laterally compressed perianth of the bilabiate type. It therefore seems a warranted supposition that *M. cuneifolia,* or at least its ancestral stock that still retained the ability to produce perianths, had the same type of perianth, and not one of the *Clasmatocolea* type. Evans (*loc. cit.*) therefore concludes that Spruce (and following him Schiffner, 1893) was in error in assigning *J. cuneifolia* to *Clasmatocolea.* The writer would express his complete agreement with this conclusion of Evans.

The last generic name used for plants variously assigned to *Mylia* is *Leioscyphus* Mitten (1855), founded for species with subopposite leaves, often connate basally with the underleaves. The type species, *L. repens* Mitt. has been studied by the writer (from material in the NYBG). It has the appearance superficially of *Lophocolea martiana* —possessing subopposite leaves (clearly alternate dorsally, however, at the base), connate at the postical base on each side with the 2-4-lobed underleaves. Since the subopposite leaves, and laterally compressed, bilabiate perianth suggest closely *Leptoscyphus,* to which the underleaf form (i.e., quadridentate type) also allies the species, the writer would agree with other students in considering *Leioscyphus* a clear-cut synonym of *Leptoscyphus.* It should be noted, however, that the genotype of *Leptoscyphus* has the rhizoids sharply restricted to the underleaf-bases, while *Leioscyphus repens,* though with the mass of rhizoids at the underleaf-bases, has some scattered rhizoids extending over the antical one-half to two-thirds of the ventral merophytes. This latter species, therefore, connects the type with scattered rhizoids (*Mylia taylori,* etc.) to the types with sharply restricted rhizoid-initials (*"M." liebmanniana, "M." cuneifolia*). In spite of this, the affinities to *Leptoscyphus* appear close enough to suggest we deal with a single genus. Further study of the various other species of these two groups is needed to determine what the pattern of rhizoid-distribution is in the group.

From the foregoing it is clear that *Mylia* (s. lat. = *Leioscyphus* sensu Stephani) includes plants with two exceedingly distinct asexual reproductive patterns (gemmae, caducous leaves), with two types of rhizoid-distribution (scattered; restricted to underleaf-bases). The writer would regard these characters as at least subgeneric and probably generic in value. They are so considered in the other genera of Hepaticae. A division of the genus, on the basis of these characters appears much more logical than the one employed by Stephani (1905, p. 1143-1144). Stephani divided the genus as follows:

I. Underleaves undivided: *L. anomalus, taylori, cuneifolius, antillanus,* etc.

II. Underleaves 2-many divided
  A. Cauline leaves dentate and bilobed: *L. fuegiensis* (and other non-New World species; *L. repens* = type of *Leioscyphus*)
  B. Cauline leaves entire
    a. Underleaves elongate: (*L. abditus, setistipus,* etc.)
    b. Underleaves small: (*L. chamissonis, chiloscyphoides,* etc.)
    c. Underleaves large: (*L. liebmannianus,* type of *Leptoscyphus,* etc.)

In the writer's opinion, Group I is wholly unnatural, since it includes four species (*L. anomalus, taylori, skottsbergii, verrucosus*) with scattered rhizoids and the ability (at least in the first two) to produce gemmae, and three species (*L. cuneifolius, antillanus, fragilis*) which produce no gemmae, but may have caducous leaves, and have the rhizoids limited to the underleaf-bases. I have seen only a few species of Group II, and these have divided underleaves with the rhizoids (as stated above) restricted either to their bases or the anterior half of the merophytes. They lack gemmae in all examined species, even though the plants may approach *M. taylori* in facies, when the lateral leaves are undivided (as in *L. liebmannianus,* the genotype of *Leptoscyphus*). The writer would suggest that Group I consists of two groups, probably generic in nature, distinct from each other in their profoundly different mode of asexual propagation, among other characters. Group II is best considered as forming a discrete, third genus, to be named *Leptoscyphus,* differing from the species in Group I not only in the general absence of asexual reproductive modes, but also in the subopposite leaves and large and elaborate underleaves. In attempting to separate Stephani's Group I from Group II, the writer does not stand alone.

Schiffner (1893, p. 76) attempted to separate Mitten's genus *Leioscyphus* from *Mylia,* on the following basis: "Leaves alternate, entire and entire-margined; amphigastria undivided, free. . . . *Mylia.* Leaves opposite, united in pairs with divided underleaves and often also on the dorsal side (of the stem). . . . *Leioscyphus.*" Schiffner's concept of *Leioscyphus* corresponds closely with Stephani's Group II, and he would restrict *Mylia* to three species of the temperate and cold regions of the northern hemisphere (*M. taylori, anomala, verrucosa*), but then after listing these three he goes on to state that "Die 3. Art ist *M. antillana* Carr. & Spr." This last species is very close to *M. cuneifolia,* which species Schiffner incorrectly places in *Clasmatocolea,* following the example of Spruce. The attempt by Schiffner to restrict *Leioscyphus* to opposite-leaved species is unfortunate. Firstly, the type of *Leioscyphus* (*L. repens* Mitt.) has, as is evident from Mitten's figures, and from actual material, slightly alternate leaves, with the dorsal insertions of the leaves not ending opposite each other. The other species cited under *Leioscyphus* by Schiffner also has at best subopposite leaves (*L. fragilifolius* (Tayl.) Spr. = *L. liebmannianus* G.), as is evident from Schiffner's figure (fig. 48A). The validity of *Leioscyphus,* thus restricted, is no greater than the hypothetical generic validity of the *Lophocolea martiana* complex would be, if separated from *Lophocolea.* In both cases, with decurrence of the underleaf-bases, and fusion of the decurrent portions with the postical leaf-bases, an opposite leaf-insertion is superficially simulated.

However, the writer would agree with Schiffner that the divided underleaves (usually quadridentate or quadrilobed), which tend to be connate with the lateral leaves on one or both sides, of the species of Stephani's Group II, are suggestively different from those of *Mylia* (s. str.). Of more significance, the species of Stephani's Group II (= *Leioscyphus,* sensu Schiffner), never produce gemmae and rarely caducous leaves (as far as known to the writer). Stephani (*loc. cit.,* p. 1142) states under *Leioscyphus* (s. lat.) "Propagula foli-

orum hyalina bicellularia." However, he mentions them only for *M. anomala* (and they occur also in *M. taylori,* and probably in the other members of that complex). They do not occur in the *M. cuneifolia* complex, nor in *Leioscyphus* (s. Schiffner).

Evans (1898, p. 426) has also pointed out that the attempt to separate *Leioscyphus* from *Mylia* on the basis of opposite leaves "does not hold, as there are acknowledged species of *Leioscyphus* (*e.g., L. chiloscyphoides*) with alternate leaves." Evans concludes that the underleaf distinction between the two groups "seems hardly sufficient to separate genera" and therefore merges the two groups under the name *Mylia.* However, the underleaf differences are correlated with phylogenetically important differences in asexual reproduction (*Mylia* s. str., with gemmae; *Leioscyphus* [at least *L. fragilifolius*] with caducous leaves), and apparently at least with a tendency towards differences in distribution of rhizoid-initials, and to some degree in the position of the leaves. Furthermore, it must be emphasized that during the last half century our generic concepts in Hepaticae, as in other plant groups, have perceptibly narrowed, leading to the conclusion that these differences are sufficient to probably warrant distinct genera.

KEY TO GENERA OF MYLIA (s. lat.)

1. Lateral leaves and underleaves both entire; with some specialized means of asexual reproduction; lateral leaves quite free from the underleaves; largely northern hemisphere, but south to South America.[7] 2
   2. Asexual reproduction by fasciculate 2-celled gemmae; vegetative leaves orbicular; the gemmiparous leaves more or less elongate; cells over 45 μ; rhizoids dense, at bases of leaves and underleaves, some $\pm$ scattered over postical stem-surface. Essentially boreal and arctic-antarctic. ....Genus *Mylia* Gray (*M. taylori,* type)
   2. Asexual reproduction by means of caducous leaves; leaves more or less uniform, more or less obcuneate; cells 18-20 x 25 μ; rhizoids restricted to bases of underleaves, few. Subtropical and tropical in derivation. ....Genus *Anomylia* g. n. (*L. cuneifolius,* type)
1. Underleaves (and sometimes lateral leaves) divided and/or ciliate, the underleaves usually quadrilobed or quadriciliate; without gemmae, and with leaves not caducous (ex. in *L. fragilifolius*); lateral leaves normally connate at postical base with the decurrent lateral bases of the underleaves.[8] Largely antipodal. ....Genus *Leptoscyphus* Mitt. (*L. liebmannianus,* type)

As thus restricted, *Mylia* may be diagnosed as follows: Plants subsimple to sparingly branched, with lateral axillary branches, and frequently *producing furcate, pseudodichotomous terminal branches, robust,* 2-10 cm long x 1.5-3 mm wide, decumbent to moderately ascending in growth (when crowded). *Stems uniform;*

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[7] *Mylia skottsbergii* (St.) comb. n. (= *Leioscyphus skottsbergii* Stephani, Bull. Herb. Boissier 5(12):218, 1906) has bilobed leaves, and comes from the Antarctic (Georgia); this possibly does not represent the genus *Mylia,* which is otherwise boreal and subarctic.

[8] As noted previously, in this taxon the rhizoids are restricted to the underleaf-bases in some species (*M. liebmanniana*), while in others they are largely restricted to a dense tuft at the bases of the underleaves, with a few rhizoids scattered over the acroscopic half of each ventral merophyte (in *M. repens* (Mitt.)).

without differentiation into leafless stoloniferous stems and leafy stems, bearing clearly alternate leaves. Stems rather fleshy, *almost uniform in structure,* the cortical cells hardly differentiated from the medullary, collenchymatous like the medullary cells and not tangentially flattened, not equally thick-walled, *strongly elongated* (ventral cortical cells *ca.* 23-27 μ wide x 140-260 μ long, leptodermous and convex; dorsal cortical cells similar, 23-28 (30-40) μ wide x (100-180) 250-400 μ long). *Rhizoids in dense masses,* occurring largely in a fascicle at bases of leaves and bases of underleaves, *a few indiscriminately over the postical stem-surface. Leaves alternate,* orbicular, *entire* (with development of gemmae becoming somewhat to strongly elongate), with antical margin not reflexed, the cnemis thus absent, inserted by an oblique and scarcely arched line, the dorsal and postical bases both essentially non-decurrent. *Cells very large,* usually 45-55 μ in the leaf-middle, becoming larger in gemmiparous regions, *strongly collenchymatous, with bulging trigones;* oil-bodies several (5-12 [16]) per cell, each formed of many small or few large, protruding globules, papillose or segmented in appearance. *Underleaves distinct, rather large, entire, lanceolate, quite free on both sides from the lateral leaves. Asexual reproduction by 2-celled gemmae* produced in fascicles from the upper leaves.

Dioecious. Female plants with terminal inflorescences; with suborbicular to ovate bracts; bracteole relatively small, undivided, not connate with the bracts. Perianth terminal, entire to ciliate at mouth, strongly laterally compressed near mouth but the keels not winged, the wide mouth essentially truncate; no perigynium; usually with subfloral innovations. Male plants with androecia becoming intercalary on main shoots; *antheridia (1) 2-4 (5) per bract, stalk 1-seriate;* bracts somewhat similar to leaves, little smaller in size, but saccate at base. Capsule short-ovoid, the walls (3-) 4-stratose; epidermal layer with usually nodular thickenings (*i.e.,* radial bands), which may extend onto the tangential walls (then with incomplete semiannular thickenings); inner layer with $\pm$ complete or incomplete semiannular thickenings. Spores rather large (15-20 μ), their diameter *ca.* 1.5-2$\times$ that of the bispiral elaters. Seta *ca.* 10 cells across, with *ca.* 24 epidermal cells, $\pm$ larger than inner cells.

Genotype.—M. taylori (Hook.) Gray (= *Jungermannia taylori* Hooker).

The genus is essentially subarctic to arctic-antarctic in distribution, with two species (*M. anomala, M. taylori*) distributed in North America and Europe; the latter eastward to Japan. A third (*M. verrucosa*) in Siberia to Japan. A fourth species (*M. skottsbergii*), very doubtfully congeneric, is antarctic in distribution, giving the genus a bipolar distribution. The few species appear to fall into two sharply discrete sections.

Section 1. ANOMALAE: Oil-bodies coarsely segmented, relatively small; cuticle smooth; perianth-mouth subentire; gemmiparous leaves elongate, lanceolate, pointed. (*M. anomala.*)

Section 2. VERRUCOSAE: Oil-bodies ellipsoidal, formed of numerous minute, not protuberant globules, botryoidal, opaque in appearance; cuticle coarsely, obviously sculptured; perianth-mouth shortly to longly ciliate; gemmiparous leaves short-ellipsoidal, never pointed (*M. taylori* and *M. verrucosa*). Judging from Plate VI, figs. 12-13, in Hattori (1951a) *M. verrucosa* and *taylori* are nearly identical as regards the form and nature of the oil-bodies.

KEY TO NEARCTIC SPECIES

1. Cuticle smooth; oil-bodies coarsely-segmented, irregular in shape, the individual segments protuberant; odorless when alive; gemmiparous leaves becoming lanceolate-pointed; pigmentation fulvous to brownish, with little or no reddish; perianth-mouth subentire; usually over *Sphagnum*. ....*M. anomala*
1. Cuticle sculptured into polygonal, coarse plates, appearing fissured; oil-bodies nearly smooth, opaque, nearly filling lumen, formed of numerous small non-protuberant globules; aromatic when living; gemmiparous leaves becoming slightly ellipsoidal to rounded-rectangulate, never pointed; pigmentation, if present, purplish-red; perianth-mouth ciliate; over shaded rocks and decaying logs. ....*M. taylori*

MYLIA ANOMALA (Hook.) S. F. Gray
Figs. 2-3

Jungermannia anomala Hooker, Brit. Jungerm. pl. 34, 1816.
Mylia anomala (Hook.) S. F. Gray, Nat. Arr. Brit. Pl. 1:693, 1821; Schuster, Amer. Midl. Nat. 49(2):410, fig. 12:1, 13:8, pl. 35:4-8, 1953; Müller, Rabenh. Krypt.-Flora, Ed. 3, 6:883, fig. 312, 1956.
Jungermannia taylori var. *anomala* Nees, Naturg. Eur. Leberm. 2:455, 1836.
Leptoscyphus anomalus Mitt., Lond. J. Bot. 3:358, 1851; Lindberg, Rev. crit. Florae Dan. Acta Soc. Sc. Fenn., 10:40, 1875; Müller, Rabenh. Krypt.-Fl. 6(1):788, 1911.
Mylia taylori var. *anomala* Carr., Brit. Hep. 68, 1875.
Coleochila anomala Dumort., Hep. Eur. 106, 1874.
Aplozia anomala Warnstorf, Krypt.-Fl. Mark Brandenburg 1:144, 1902.
Leioscyphus anomalus Stephani, Spec. Hep. 3:16, 1905; Bull. Herb. Boissier, Ser. 2, 5:1144, 1905.

Plants closely decumbent to prostrate, creeping over *Sphagnum* or forming turf-like mats over peat, often in dense, luxurious patches, in dense shade pure green, but usually (in sun) *yellowish-brown to fulvous to somewhat reddish-brown.* Shoots usually simple, usually innovating below perianths, 2.4-3 mm wide and 2-3 cm long. Stem stout, 440-600 μ wide, 9-14 cells high, rather fleshy, pale usually, with poorly developed cortex, the cortical cells only little smaller than medullary in cross-section (28-36 μ in diameter x 140-350 (400) μ long), relatively thin-walled; medullary cells strongly elongate, rounded-polygonal in cross-section, thin-walled but with distinct trigones, 32-48 μ in diameter. Rhizoids abundant, forming dense felty masses, long, often tufted, arising largely near postical leaf-bases and from underleaf-bases, a few indiscriminately from postical stem surface, occasional ones arising from surface or margins of the basal one-fifth to one-half of the free underleaves (Fig. 3:11). Leaves clearly

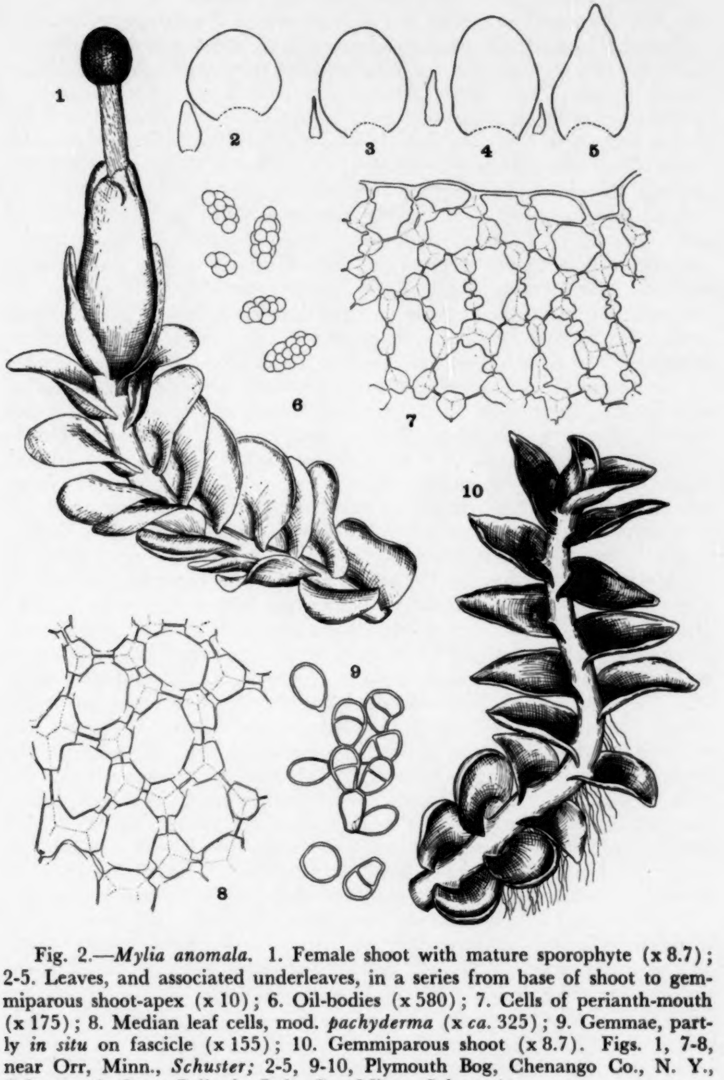

Fig. 2.—*Mylia anomala.* 1. Female shoot with mature sporophyte (x 8.7); 2-5. Leaves, and associated underleaves, in a series from base of shoot to gemmiparous shoot-apex (x 10); 6. Oil-bodies (x 580); 7. Cells of perianth-mouth (x 175); 8. Median leaf cells, mod. *pachyderma* (x *ca.* 325); 9. Gemmae, partly *in situ* on fascicle (x 155); 10. Gemmiparous shoot (x 8.7). Figs. 1, 7-8, near Orr, Minn., *Schuster;* 2-5, 9-10, Plymouth Bog, Chenango Co., N. Y., *Schuster;* 6. Great Palisade, Lake Co., Minn., *Schuster*).

alternate, the succubously oblique line of insertion little acroscopically arched, approximate to moderately imbricate, somewhat to strongly narrowed basally, not decurrent postically, short-decurrent antically, the lower usually spreading or erect-spreading, the upper spreading to suberect. Lower, non-gemmiparous leaves almost *perfectly orbicular,* with the line of insertion *ca.* one-half the median, maximal width of the leaf; leaves *ca.* 1450-1500 μ wide and long; *upper leaves* (*of gemmiparous shoots*) *progressively somewhat more elongate,* at first ovate and to *ca.* 1300 μ wide x 1440 μ long, *becoming distinctly ovate-lanceolate to lanceolate distally* (and *ca.* 1100-1125 μ wide x 1500-1750 μ long); leaf-margins varying from nearly plane to slightly incurved adaxially—the leaves thus varying from nearly flat to somewhat adaxially concave and saucer-like; gemmiparous leaves often somewhat canaliculate, with the postical and antical margins both adaxially recurved. Cells very distinctly to excessively collenchymatous, the trigones bulging to so strongly bulging that the lumens of the cells are connected merely by pits; cells near leaf-apex and leaf-middle from 45-50 x 50-60 μ, polygonal, of the base 50-55 x 60-70 μ or even larger, of the margins mostly 44-50 μ; *cuticle smooth;* oil-bodies 5-8, occasionally in the larger cells 12-20 per cell, irregularly spherical to ovate, hyaline, distinctly formed *of relatively few, coarse, protuberant globules or segments* (each *ca.* 1.5-3 μ), varying from 5-7 x 7-8 μ to a maximum of 7-8 x 10-12, rarely 14-18 μ. *Underleaves relatively large,* present throughout, varying from one-fourth to one-half the leaf-length, the larger 500-680 μ long x 250-300 μ wide, mostly lanceolate to narrowly lanceolate, some tipped by a cilium 2-5 cells long, undivided, usually nearly obscured by the rhizoids. *Asexual reproduction usually abundantly present* by means of fasciculate gemmae, mostly 2-celled, from apices of upper, lanceolate leaves (the cells of these apices *very large and elongate,* to 32-40 x 100-130 μ); gemmae *ca.* 35 μ to 40 x 50 μ, greenish (their walls colorless), spherical to broad-ellipsoidal.

Dioecious. Male inflorescences becoming intercalary, on main stems, consisting of 4-7 pairs of bracts; bracts similar to leaves, but somewhat ovate, the basal one-half strongly concave and suberect, the distal portion spreading; antheridia 2, subglobular to short-ovoid, the stalk uniseriate. Female inflorescences terminal on main shoots; bracts like leaves, ovate to roundish-ovate, erect and somewhat sheathing perianth at base, erect-spreading distally, with the tips often somewhat recurved; bracteole distinct, large, lanceolate. Perianth at least ½ emergent at maturity, weakly compressed below but strongly laterally compressed and flattened above, somewhat (but little) narrowed to the bilabiate, relatively wide mouth; *mouth subentire to crenulate.* Seta 580 μ in diameter, 10-11 cells across; epidermal cells in *ca.* 24 rows, little larger than inner cells; inner cells each 62-75 μ in diameter; walls thin except tangential ones of outer layer. Capsule short-ovoid; valves 4-stratose, the outer layer with radial (nodular) thickenings; inner layer with incomplete semi-annular bands. Elaters 9.2-12 (14) μ thick x 100-140 μ; spirals 3-3.5 μ wide. Spores 15-20 (22) μ,

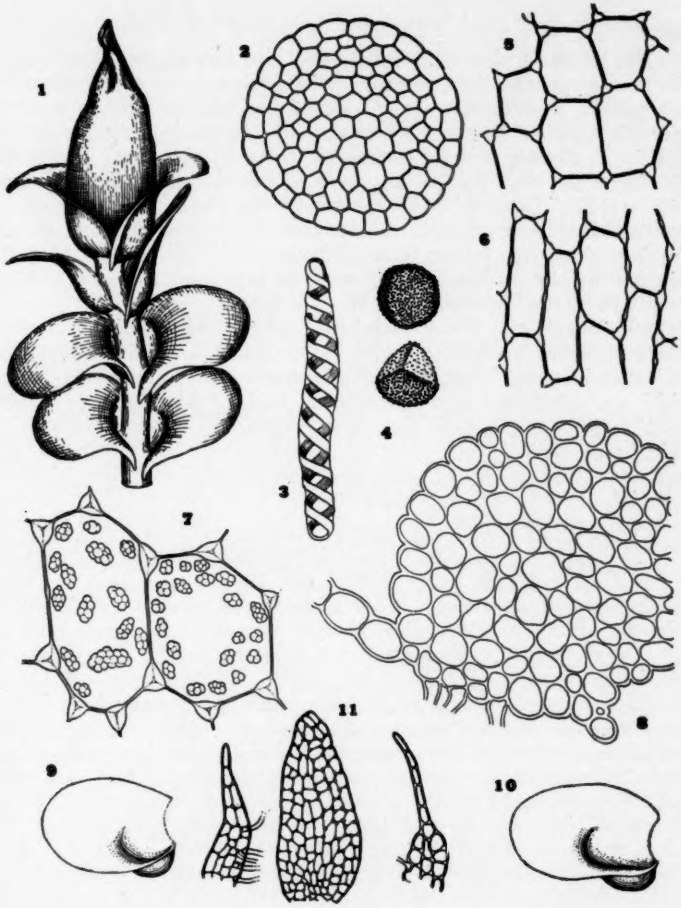

Fig. 3.—*Mylia anomala*. 1. Antical aspect of shoot with mature perianth (x *ca.* 9); 2. Seta cross-section (x 53); 3. Elater (x 540); 4. Spores (x 540); 5. Median cells of leaf (x *ca.* 135); 6. Cells near apex of gemmiparous leaf (x *ca.* 135); 7. Two median cells with oil-bodies (x 345); 8. Stem, medium-sized, in cross-section (x 112); 9-10. Male bracts (x *ca.* 11); 11. Underleaves (x 40). (Figs. 1-4, 9-10, Bog near Orr, Minn., *Schuster;* 5-6, 11, Plymouth Bog, Chenango Co., N. Y., *Schuster;* 7, Great Palisade, Lake Co., Minn., *Schuster;* 8. Malloryville Bog, Tompkins Co., N. Y., *Schuster.*)

averaging 17-18 μ, the convex outer wall verruculose-rugose, the inner faces with $\pm$ scattered papillae.

Type.—Holt, England (presumably in the Hooker Herbarium).

Variation.—Although a widespread and locally abundant species, the ecological tolerances are narrow enough so that the species does not exhibit a disturbing amplitude of variation. Shade forms are greenish and somewhat lax-leaved, with relatively long internodes; sun forms develop shorter internodes, denser leaves, and a brownish pigmentation; they furthermore become very strongly pachydermous. Müller (1905-1916, p. 788) states that, as a rule, the trigones are smaller in *M. anomala* than in *M. taylori.* However, I find that in the form from sunny bogs (mod. *colorata-densifolia-pachyderma*) the trigones may be extremely large, with the lumen consequently reduced to pits along the intervening walls.

Schiffner (1908) has grouped the various "forms" of *M. anomala* into two series (gemmae-producing forms that are habitually sterile, and round-leaved forms, devoid of gemmae, reproducing sexually), which are subdivided into forms on the basis of adaptation to varying combinations of moisture and light conditions. There seems to be little or no basis for the primary division, since both perianth- and capsule-bearing specimens often grow intermingled with gemmiparous material. Moreover, the various "forms," as Müller (*loc. cit.*, p. 791) indicates, are modifications resulting from differing environmental conditions. The series of forms and varieties proposed by Schiffner, therefore, lack taxonomic significance.

Ecology.—The ecology of this species is treated in detail by Schuster (1953, p. 410). The species essentially occurs under analogous conditions in two very different habitats. In peat bogs, it almost invariably occurs over *Sphagnum,* which it often kills off by its luxuriant growth, then forming thick, peaty, pure mats; here it is a member of the *Mylia-Cladopodiella* Associule. Under the most moist conditions, *Cladopodiella fluitans, Cephaloziella elachista,* and various *Cephalozia* species (*compacta, connivens, pleniceps,* etc.) are consociated, occasionally with *Microlepidozia setacea, Riccardia latifrons, Scapania irrigua* and *S. paludicola.* In more xeric sites, such as the apices or upper slopes of large *Sphagnum* hummocks, in full sun, *Mylia* grows with *Microlepidozia setacea, Calypogeia sphagnicola, Cephalozia loitlesbergeri,* occasionally *Cephaloziella subdentata.* A second habitat is over *Sphagnum* and peat on moist ledges, especially in very moist environments (as on the north or northwest-facing sides of cold lakes). Here it is a member of the *Mylia-Odontoschisma* facies, of the *Mylia-Cladopodiella* Associule (Schuster, 1957). Consociated are *Odontoschisma denudatum, Cephaloziella subdentata, Lophozia incisa* and *silvicola* (occasionally the pigmented *porphyroleuca*-simulating forms), occasionally *L. wenzelii* (often the "*confertifolia*" type), and rarely *Lophozia kunzeana; Cephalozia loitlesbergeri* and occasionally *C. leucantha* or *media* are also consociated.

At the northern edge of its range, at the juncture with the Tundra in northern Quebec, *Mylia* is found over peat on margins of pools, in raised sand beaches at river mouths, with *Cephaloziella elachista, Cephalozia leucantha, Lophozia wenzelii, L. grandiretis, Cephalozia loitlesbergeri, C. pleniceps, Lophozia kunzeana, Scapania irrigua* and *Geocalyx graveolans,* and "above a temporary snowbank," among *Sphagnum, Lophozia atlantica* and *Calypogeia* (Schuster, 1951).

In addition to the preceding, relatively frequent, modes of occurrence, *M. anomala* appears to be widespread in the Lake Superior region on seepage-moist, insolated steep, eroding sandstone ledges and bluffs (as at Miners Castle, Pictured Rocks, Mich.). Here the plant occurs as a member of the *Gymnocolea-Cephalozia bicuspidata* Associule (see Schuster, 1957, p. 263), which usually occurs around rock-pools and on acid, sunny rocks, with various members of the *Empetrum-Vaccinium* heath (at Pictured Rocks, *E. nigrum* is associated). In addition to the *Gymnocolea* and *Cephalozia, Odontoschisma denudatum, Cephalozia media, Lophozia silvicola, L. incisa* and *L. groenlandica* are associated at Pictured Rocks.

Distribution.—Almost ubiquitous in bogs in the Coniferous Zone of northern North America and Europe, eastward into Siberia, becoming rarer in the "Hochmoore" on the peaty ridges of rocky mountain tundra, as on Hamline Ridge, Mt. Katahdin, Maine; there with *Calypogeia sphagnicola;* and at Caribou Spring, Mt. Katahdin; there with *Lophozia wenzelii, Cephalozia, Lophozia kunzeana.* Becoming relatively rare in the isolated bogs of the Transition Zone, and relatively rare in the Arctic Tundra. According to Buch and Tuomikoski (1955) circumboreal, although in east Asia known only from Kamtschatka (Arnell, 1927).

Westward ranging from ALASKA: Juneau, Kalsina Valley and Metlakatla! (Frye and Clark, 1943); Kotsina Valley (Clark and Frye, 1942) to the YUKON: Dawson; Hunker Creek!, Bonanza Creek! (Evans, 1903), southward to BRITISH COLUMBIA: Lytton (Macoun, 1902), Yoho Valley (*Macoun 1904!*) and ALBERTA: between Dunvegan and St. John, Peace R. (Macoun, 1902); Nordegg Forest Reserve (Frye and Clark, 1943); Loggan (*Macoun, 1904!*); southward to WASHINGTON: Hamilton!; Pacific Beach!; Seattle (Frye and Clark, 1943); Mt. Constitution(*Wentworth, 1923!*); Westport (*Foster, 1908!*); Ashford (*O. D. Allen, 1905!*).

Eastward as follows: QUEBEC: Cairn Island, Richmond Gulf, Great Whale R., on E. coast of Hudson Bay (Schuster, 1951, based on *Marr* 630!, 661d!); R. à Martre, above Lac aux Sables!; La Tuque at Lac Bourgeois; Montmorency R., St.-Arsène, near R.-du-Loup; Mt. Albert; Lac Salé, Anticosta I. (Lepage, 1945); Rupert R. near Sand Lake, 76°20′ W. (Lepage, 1945); Lake Hubbard, with *Lophozia atlantica, Polytrichum juniperinum* var. *alpestre* (Kucyniak, 1949). NEWFOUNDLAND: Hoggan's Pond, Avalon Distr.; Push-through and Port aux Basques, S. Coast; Port au Choix, Cook Harbor and St. Anthony, N. Peninsula; Kitty's Brook, C. and N.E. Nfld. (Buch and Tuomikoski, 1955). NOVA SCOTIA: Barrasois!, Barrasois Barrens and Ingonish!, Cape Breton I.; Halifax Co. (Brown, 1936; Nichols, 1916); near Yarmouth (*Macoun, 1910!*). NEW BRUNSWICK: Bog near Spruce Lake (*Nichols, 1917!*);

Campobello (*Farlow, 1898!*); Grand Manan (*Weatherby, 1926!*). ONTARIO: Cochrane; Sudbury; Lake Timagami; Thunder Bay (Cain and Fulford, 1948). MAINE: Matinicus Island (Lorenz); Round Mt. Lake, Franklin Co.; Mt. Desert I. (*Lorenz!*); Schoodic Lake (*Evans, 1908!*); Cumberland (*Collins and Chamberlain* 1627!); peat bog near Roaring Brook Campground, base of Mt. Katahdin (*Schuster* 32925a, 32951a, 32927, 32925, 32954, 32940, 32931, 32928a); Hamline Ridge Trail, 32-3800 ft., Mt. Katahdin (*Schuster* 15997a, 15999, 15997, 15998b); Caribou Spring, Thoreau Spring, on tableland, Mt. Katahdin, *ca.* 4900-5000 ft. (*Schuster* 15950, 32975). NEW HAMPSHIRE: Mt. Chocorua!; Franconia Mts. (Evans, 1908); Lonesome Lake, Mt. Lafayette (Lorenz, 1908; *Schuster*); Eagle Lake, Mt. Lafayette (*Evans, 1908! Schuster*); edge of Hochmoor, at *ca.* 3200 ft., Mt. Monadnock (*Schuster* 19453a); Star Lake, Mt. Madison (*Evans, 1917!*); Greeley Pond, Waterville (*Evans, Aug. 27, 1911, c. caps.!*). VERMONT: Jericho, with *Lophozia marchica, Scapania* irrigua (*Evans!*); Willoughby (*Lorenz!*); Brandon (*Dutton* 1255! 2191!); Elgin Pond, Wallingford, *Lorenz, 1916!*). MASSACHUSETTS: Holden, with *Cladopodiella fluitans;* swamp S. of Sesachacha Pond, Nantucket I.; Cedar Swamp, Brookline (*Lorenz, 1916;* with *Microlepidozia setacea*); Bog near Hawley, SW. Franklin Co. (*Schuster* 40121!, with *Microlepidozia setacea, Cephaloziella elachista, Cladopodiella,* etc.); Rutland Pond, Holden (*Greenwood, 1914!*). CONNECTICUT: Woodbury, Litchfield Co.!; Bethany! and New Haven!; New Haven Co. (Evans and Nichols, 1908); Norfolk (*Evans, 1913!*); Southington (*Evans, 1915!*); New Fairfield (*Nichols, 1912!*); Brookfield (*Lorenz, 1910!*); Bingham Pond, Southington (*Evans, 1911!*); Suffield (*Nichols, 1911!*); Berlin (*Nichols, 1910!*); N.E. of Salisbury (*Lorenz, 1916!*). NEW YORK: McLean Bogs, (*Andrews; Schuster and Rader*), Malloryville Bog (*Schuster*), both in Tompkins Co.; swamp near Crystal Lake, Cattaraugus Co. (*Boehner!*); Lake Meacham (*Lorenz, 1905!*); Bergen Swamp, Genesee Co. (*E. J. Hill; Schuster*); Junius Peat Bogs, Seneca Co. (*R. M. and Erwin Schuster*); Jamesville Rd., Onondaga Co. (Goodrich, 1912 p. 23, as *M. taylori*); Plymouth Bog and Reservoir, near S. Plymouth, Chenango Co. (*Schuster and Winne*); Lake George; southern W. Fort Ann!; *Sphagnum* marsh N. of Glen Lake, Warren Co. (*Burnham!*). PENNSYLVANIA: near Sulphur Spring, Warren Co. (Lanfear). NEW JERSEY: near Closter, Bergen Co., in peat bog (Austin, Hep. Bor.-Amer. No. 25, 1873). WEST VIRGINIA: Pocahontas Co. (Ammons, 1940); Cranberry Glades (*Gray, 1923!*).

Westward occurring to MICHIGAN: Burt Lake, Cheboygan Co.; Eagle Harbor, Keweenaw Co.; Scotts; Isle Royale, Keweenaw Co.!; Miners Castle, Pictured Rocks, Munising Co. (*Schuster* 39101, etc.); Luce and Chippewa Cos. (Steere, 1937, 1940, etc.). WISCONSIN: Black R., Superior, Stone's Bridge on Brule R., in Douglas Co. (Conklin, 1929); east-facing edge of Sand I., Apostle Isls., Bayfield Co. (*Schuster* 17799); Superior (*Conklin, in* Haynes, Amer. Hep. 93!). MINNESOTA: Porcupine I.; Pigeon R., Lake Superior; Beaver Dam on Hungry Jack Trail; Sailboat I., Lucille I., Belle Rose I., Long I., Big Susie I., all in Susie Isls., Grand Portage marl bog, Big Bay at Hoveland, all in Cook Co. (*Schuster*); bog near Jaynes, and 5 mi. W. of Togo, both in Itasca Co. (*Schuster*); bog 4 mi. SE. of Ericsburg, and bog at Black Bay, near Island View, Koochiching Co. (*Schuster*); bog at Kerrick, Pine Co. (*Schuster*); 8 mi. SW. of Gheen; bog 2 mi. N. of Orr; bog 1-2 mi. E. of Celina, all in St. Louis Co. (*Schuster*). (See Schuster 1953, 1957).

Differentiation.—A strongly isolated species that need never be confused with any other species (however, misdetermined (in Cain and Fulford, 1948) for *Jungermannia lanceolata* by M. Fulford; at

least part of these misdeterminations corrected by Cain to *Mylia*). At one time considered merely a variety of *M. taylori,* but not even closely related to that species. It differs from the latter abundantly in its ecology, in the smooth leaves, the development of acute apices of the leaves with gemmae-formation (Fig. 2:10), the brownish (never reddish) pigmentation, the segmented and hyaline oil-bodies (Fig. 3:7), the subentire perianth-mouth (Fig. 2:7).

The European authors often stress the supposedly constant sterility of this species as a diagnostic feature. For example, Warnstorf (1903, p. 145) states that "*A. anomala* ist, soweit bis jetzt bekannt, fast ausschliesslich auf vegetative Vermehrung durch reichliche Keimkörnerbildung angewiesen, während sich *A. taylori* nur auf geschlechtlichem Wege fortpflantzt. . . " Schiffner (1910, p. 4) also emphasizes the supposed rarity of gemmiparous phases of *M. taylori,* distinguishing them as a var. *propagulifera* that is surely without merit. These distinctions appear induced by environmental and not genetic causes, hence appear of very little, if any, value. Furthermore, Schuster (1953) has shown that, at least in the Great Lakes area, *M. anomala* often produces capsules, which mature in August and September.

The anatomy of the capsule-wall appears to offer more valid means of separating these two species. Schiffner (1908, p. 60) has briefly described these differences, which I can largely substantiate. In *M. anomala* the inner cell layer of the capsule-wall bears, at least in the median and distal portions of the valves, only incomplete and sparingly developed tangential bands; in *M. taylori* (see p. 51) these cells bear numerous and dense, generally complete tangential bands. The epidermal cells also differ: in *M. anomala* they bear "normal" nodular thickenings along the longitudinal walls, *i.e.,* possess simple vertical, or radial bands along the radial walls; in *M. taylori* the outer extensions—along the tangential walls—of the radial bands are in large part coalescent or anastomose, resulting in what Schiffner describes as an "eigentümlich verworrenes Bild." This peculiar modification is described in detail on p. 50.

MYLIA TAYLORI (Hook.) S. F. Gray

Fig. 4

Jungermannia taylori Hooker, Brit, Jungerm., pl. 57, 1816.
Mylia taylori (Hook.) S. F. Gray, Nat. Arr. Brit. Pl. 1:693, 1821 (as *Mylius*); K. Müller, Rabenh. Krypt.-Fl. Ed. 3, 6:879, figs. 308-309, 310a, 1956.
Mylia taylori Lindberg, Hep. in Hib. lect. 525, 1874.
Aplozia taylori Dumort., Rec. d'Obs. 16, 1835.
Leptoscyphus taylori Mitten, London J. Bot. 3:358, 1851.
Leioscyphus taylori Mitten, *in* Hooker, F. antarct. 2(2):134, 1855.
Coleochila taylori Dumort., Hep. Eur. 106, 1874.
Jungermannia reticulato-papillata Steph., Mem. Soc. Nat. Cherbourg 29:215, 1892.

Plants robust, usually in thick (3-10 cm) tufts or sods, almost invariably *carmine-red to purplish-brown pigmented* (mod. *colorata*),

at least on distal parts of upper leaves, even when growing in very diffuse light. Plants recumbent to strongly ascending (when crowded) up to 3-4, occasionally 4-5 mm wide x 3-6, occasionally 8-12 cm long, the male plants slightly smaller (2.7-3.5 mm wide). Stems simple or sparingly branched, often narrowly furcate, flexuous, rather stout (to 480-550 μ in diameter); branches in part terminal; cortex of rather pellucid, $\pm$ thin-walled, rectangulate cells, (20-28) 30-40 μ wide x (80) 100-180 (200) μ long, whose external walls are convex, very thin, the internal walls and those of adjacent medullary cells slightly thicker; medulla *ca.* 10 cells high, the cells subequal in diameter to cortical (32-40, a few to 48 μ) in diameter; no mycorrhizae. *Rhizoids forming a dense, felted mat,* usually brownish, *long,* scattered, densest at postical bases of leaves and below underleaves, often several inserted on the underleaves. Leaves at maturity nearly horizontally spreading, *the upper characteristically erect-appressed,* subimbricate to moderately imbricate, inserted by a moderately oblique, scarcely acroscopically arched line of insertion, virtually undecurrent postically, short-decurrent antically, from broadly ovate (*ca.* 1500-1600 μ wide x 1600-1800 μ long) to orbicular (to 2400 x 2400 μ); leaves from slightly concave, at least at median base, to somewhat convex above the base (due to the somewhat reflexed antical margin, and *often deflexed apices*). *Cells very large,* 34-38 up to 40-45 μ on the margins, 40-45 x 45-60 (75) μ in the leaf-middle, somewhat larger usually near base, strongly collenchymatous with bulging trigones, the *trigones usually nodulose,* sharply defined, with intervening walls very thin; *cuticle roughened, divided into irregular, coarsely polyhedral plates; oil-bodies very large, opaque, grayish or brownish-gray, often obscuring most of lumen,* (5) 7-12 (16) per cell, ellipsoidal or less often subspherical, *appearing papillose,* due to the numerous minute (less than 1.3-1.5 μ) included globules that slightly protrude externally, varying from 7-9 x 9-10 μ to 7-10 x 13-16 (18-20) μ. *Underleaves slenderly lanceolate to subulate, ca.* 425-500 μ long x 90-100 μ wide, usually nearly hidden in the rhizoid-mat. Asexual reproduction frequent but *not copious,* by means of fasciculate gemmae arising from the margins of more or less *ovate* (*but never lanceolate*) *leaves with rounded apices;* gemmae 1-2-celled, usually thin-walled, oblong to oval, 30 μ to 25-30 x 40-45 μ, green to somewhat reddish-brown (in mod. *colorata*).

Male plants with intercalary androecia, of 4-8 pairs of *imbricate bracts,* similar to those of *M. anomala;* saccate base of each bract with 2-3, more rarely 1 antheridium, the distal half of bracts strongly spreading. Female plants with perianth terminal; often with 1 or 2 subfloral innovations; bracts somewhat larger than leaves, broadly ovate to subrotundate, *ca.* 2250 μ wide x 2150 μ long or larger, usually sheathing perianth at base and concave and erect, spreading distally and sometimes reflexed apically; bracteole large, lanceolate. Perianth to 3000 μ long x 1500 μ broad, smooth as in *M. anomala,* but the *mouth ciliate with cilia (2-3) 4-6 cells long;* cells of cilia nearly or quite smooth, the lower 20-25 x 22-35 μ, the terminal cells commonly

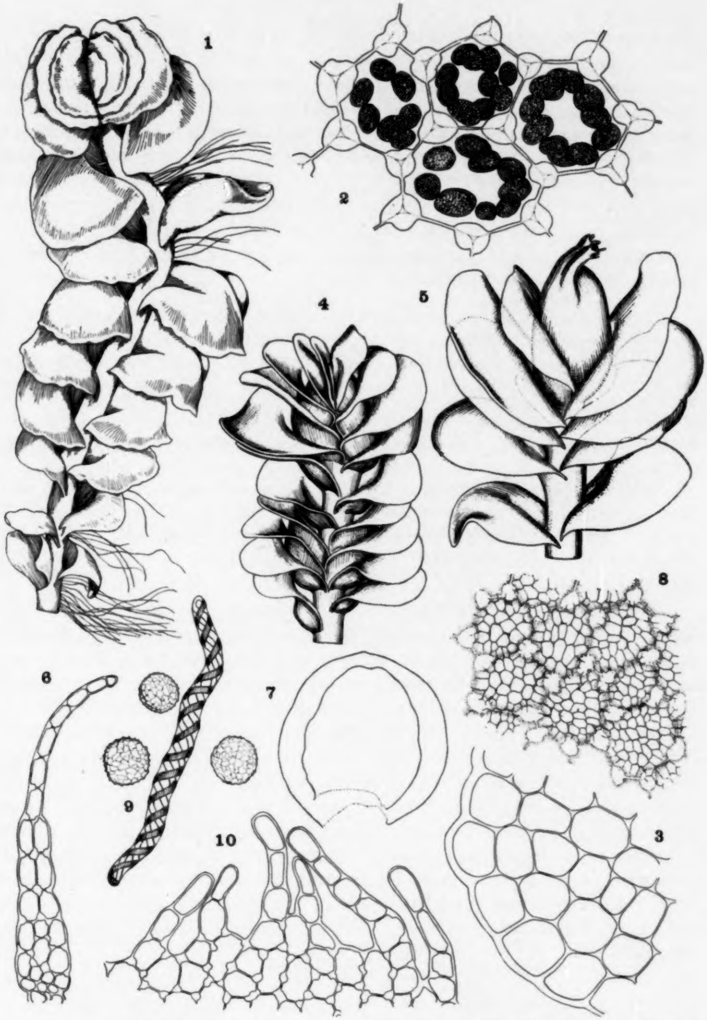

Fig. 4.—*Mylia taylori.* 1. Sterile plant (after K. Müller; x *ca.* 10); 2. Median cells, with oil-bodies (x 325); 3. Part of seta cross-section (x 150); 4. Apex of male plant (x 10.7); 5. Apex of female plant (x 10.7); 6. Underleaf (x 104); 7. Leaf, drawn within a ♀ bract (both x 14); 8. Median cells, surface view to show cuticular ornamentation (x 215); 9. Spores and elater (x 340); 10. Part of perianth-mouth (x 150). (Fig. 1, after K. Müller; 2-3, Great Whale R., Quebec, *Marr* 656c; 4-10, Mt. Katahdin, Maine, *Schuster* 17030).

somewhat clavate and larger, *ca.* 20-28 x 40-45 (48) μ; perianth surface with cuticle like that of leaves. Capsule as in *M. anomala,* purplish-brown, the *wall 3-4- stratose,* epidermal cells sometimes with partial tangential extensions of the radial (nodular) bands; inner cell layer with narrow, ± complete, *often 2-3-furcate tangential bands.* Elaters 10-12 (14) μ in diameter, the two purplish spirals tightly wound; spores (16-17) 18-20 (21) μ, *finely aerolate,* the verruculose markings anastomosing. Seta of numerous cell-rows, the epidermal in 20-25 rows, often slightly larger than the interior cell-rows.

Type.—Toulagee Mt., Wicklow Co., Ireland (*Dr. Thomas Taylor*), presumably in the Hooker Herbarium.

Variation.—A very characteristic species, exceedingly stenotypic in nature, therefore not offering any problems in its recognition. The plants are almost always of the mod. *colorata-pachyderma-densifolia,* although entirely green modifications are not rare. Schiffner (1910) emphasizes the variability of the plant. However, in my opinion this variability is limited and all of an obviously environmentally-induced origin.

Schiffner has described a "var. *uliginosa*"—a modification with long internodes and often no secondary pigmentation, growing in water. Such extreme forms are exceptional, and still retain the characteristic ornamentation of the cell-walls by which the species can be distinguished from all other regional Hepaticae.

Distribution.—A widespread, circumboreal species, found from northern Europe to the central European Alps, southward to Dalmatia, but largely western in range, and very common in montane situations on the Atlantic coast, on the Faroes, but not appearing to extend southward to the Pyrenees (Allorge, 1955); recurring in the Azores (Allorge, 1950). Also in Japan (Alpine region, *fide* Hattori, 1952), and in China; reported from India. The species extends northward to the edge of the Tundra, but appears absent in the main body of the Tundra (it is frequent, however, in Alpine Tundra, as on Mt. Katahdin); it is weakly oceanic in range, and is largely absent from the continental portions of the northern Hemisphere. Evidently absent from Iceland and Greenland, although the species is still listed from Greenland in Müller (1911), Frye and Clark (1943), and Buch and Tuomikoski (1955), evidently on the basis of a report by Jensen (1898). However, Jensen (1906, p. 303) states this species has not been found in east Greenland, "the very unimportant sample, referred by me in "Mosser fra Östgrönland" to this species belongs in *Arnellia fennica.*" Macoun (1902) also cites an old, ambiguous collection from Greenland by Vahl.

In North America restricted largely to the Appalachians and the Atlantic Coast region, southward as a relict in the southern Appalachians, rarely northward to the Hudson Bay region (Schuster, 1951), and then recurring in the Pacific Coast region. In the west found as follows: ALASKA: Yakutat Bay (*Stair, 1947*); Juneau (Frye and Clark, 1943); Cordova, Ward Lake, Orca

and Thumb Bay (Clark and Frye, 1942); Hot Spring, Douglas I., Columbia Fiord, Port Wells (Evans, 1900); Morse Cove, Port Alice and St. John Harbor (Evans, 1915); Sitka (*n.c.,* 1894!); Douglas (*L. Clark, 1908!*); Virgin Bay, Prince William Sound (*W. Trelease, 1899!*); Port San Antonio (*Frye* 608!); Augustine Bay (*Frye* 575!); Shipley Bay (*Frye* 773!); Ketchikan (*Frye* 542!); Port Alice, Hecate Is. (*Frye* 787!); Juneau (*Mehner* 163!); Nicholas Bay (*Frye* 320!); Port Chatham (*Frye* 1225!); Saltery Cove (*Frye* 327!). BRITISH COLUMBIA: Stanley Park (Macoun, 1902); Lewis Island and Port Renfrew, on Vancouver Is. (Frye and Clark, 1943); Port Renfrew, Vancouver Is. (*Gibbs* 64!, 124!, 51!, 40!); Ucluclet (*J. Macoun* 47!; with *Gyrothyra underwoodiana*). ALBERTA: (Macoun, 1902, "In a bog at House Mountain, Lesser Slave Lake"; this almost surely is an error for *M. anomala,* judging from both the continental position of the station and from the habitat). WASHINGTON: "Two mi. so. Fork," Olympic Penninsula, Clatham Co. (*A. Svihla* 459!).

In eastern North America not reported to the west of the Appalachian system, except for stations on the east coast of Hudson Bay (Schuster, 1951); the report from Illinois in Frye and Clark (*loc. cit.*) based on the old list of Wolf and Hall being wholly without merit. QUEBEC: Manitounuck Sound and mouth of Great Whale R., E. coast of Hudson Bay (Schuster, 1951; based on *Marr* 648a!, 655!, 662!, 656a!, 662a!, 659!); Rupert R., above Lake Nemiskau; Ste. Anne de la Pocatière, R. Ste. Anne-des-Monts (Lepage, 1945); St. Anne (*Lepage* 100!); Mt. Albert, Gaspé (*J. A. Allen, 1881!*); Table-top Mt., Gaspé (*Collins and Fernald* 4511!); Rupert R., 76°30′ N. and 51°20′ W. (*Lepage and Dutilly* 4467!). LABRADOR: without locality (Waghorne; *fide* Macoun, 1902); Salmon Bay (*O. D. Allen* 33!, 16!). NEWFOUNDLAND: Channel (*Howe and Lang* 875!, among *Diplophyllum albicans, Calypogeia meylanii;* 806!); widespread (Avalon Distr., S. coast, W. Nfld., N. Peninsula, and W. and NE. Nfld.; *fide* Buch and Tuomikoski, 1955); Bay of Islands (*Howe and Lang* 1174!, 1161!); Quarry (*Fernald and Wiegand* 6448!); St. Anthony (*Evans, 1937!, p.p.,* with *Cephalozia leucantha*). MIQUELON I. (Macoun, 1902). NOVA SCOTIA: Pirate's Cove, Canso; Margaree, Halfway-House and Louisburg, Cape Breton I. (Macoun, 1902); Kearney's Rd., Halifax (Brown, 1936); Halfway Brook (*Macoun, 1898!*); Valley of Barrasois R. (*Nichols* 319!); Louisburg (*Macoun, 1898!*); w. of Ingonish (*Nichols* 832!); Big Intervale (*Macoun, 1898!*). NEW BRUNSWICK: Manan (*Weatherby, 1926!*). MAINE: Northwest basin, *ca.* 2800-3200 ft., Mt. Katahdin (*Schuster* 15976, 15967a, 17030, 17023); Hamline Ridge, on North Basin trail; Cleft Rock pool, above Chimney Pond, *ca.* 3000-3200 ft., Mt. Katahdin (*Schuster* 32909, 33024a); Cathedral trail, Mt. Katahdin, *ca.* 4500-4800 ft. (*Schuster* 32980, 32980b, 32980a); N. slope of Baxter Peak, *ca.* 5000 ft., Mt. Katahdin (*Schuster* 15817, 15941, 15941a); Saddle Slide, *ca.* 5000 ft., Mt. Katahdin (*Schuster* 33004, 33002, 33004a); Mt. Bigelow, Dead River (*Collins and Fernald* 1522!); Round Mt., on Snow Mt. trail (*Lorenz, 1915!*). NEW HAMPSHIRE: Franconia Mts., Mt. Lafayette (*Lorenz, 1908!*); very widespread in the Presidential Range, White Mts., from Mt. Clinton and Mt. Monroe to Mt. Adams (*Schuster*); Crystal Cascade, Mt. Washington (*Underwood and Cook, 1889!*); Mt. Adams (*Farlow, 1897!*); Bald Cap Mt., Shelburne (*Farlow, 1893!*); Mt. Lafayette, the Flume, etc. (Evans, 1917); Triple Falls, Mt. Madison (*Evans, 1917!*); Kings Ravine, near Mossy Falls, Mt. Adams (*Evans, 1917!*); Ice Gulch, Randolph (Evans, 1917!); Mt. Carrigain (*Lorenz, 1908!*). VERMONT: Haystack Mt., Windham (*Line, 1940!*); Willoughby, 1200 ft. (*Lorenz, 1903!*); Mt. Mansfield, 4200 ft. (*Lorenz, 1906!*). Mt. Killington, Sherburne (*Dutton* 461!): Brattleboro (*C. C. Frost, 1855*). NEW YORK: near summit Wittenberg Mt.,

Catskill Mts. (*Schuster* 24424a, 24718, 24304, 24305, 24429, 24460a, 24460, 24704b, 24704a, 24700, 17598, 24698, 24704, 17591); near summit of Cornell Mt., Catskill Mts. (*Schuster* 24415a, 24470, 24688, 24437, 17571, 1750, 24458a, 24458, 24459b); slope of Slide Mt., Catskill Mts., leading down to Cornell Mt., *ca.* 3700-3900 ft. (*Schuster* 17636, 17636a, 17618, 17619, 17635); Arnold Lake (*Wilson 18, 10a, 10b, 19!*); 0.5 mi. above Avalanche Gap, Mt. Marcy (*Wilson 24!*); Lake Placid, Adirondack Mts. (*Britton!*); Opalescent R., near Buckley's Clearing, Essex Co., Adirondack Mts. (*Lewis* 3882!; det. by H. N. Moldenke as *Scapania undulata!*); Whiteface Mt. (*E. G. Britton, 1896!*). Occurring as a disjunct in NORTH CAROLINA: Grandfather Mt., *ca.* 5800 ft., Avery Co. (*A. L. Andrews* 244, Aug. 15, 1919!).

The report of this species from Bergen Co., New Jersey ("among peat mosses in bog near Closter" *Austin; in* Britton, 1882) surely refers to *M. anomala.* Although reported from Rhode Island (Frye and Clark, 1943), this report is surely an error, since Evans (1913, 1923a) refused to accept the Rhode Island report. Müller (1956, p. 882) incorrectly records the species from Illinois.

The species is an excellent indicator of the Taiga Biome, dropping out almost completely before the lower edge of the Spruce-Fir Forest is reached. In the Catskill Mountains, where it is abundant locally, strictly limited to the Spruce-Fir Zone.

Ecology.—Commonly only in montane areas, and on acidic rocks, although Müller (1905-1916) states he has also found it over limestone cliffs, where he admits it is not found directly on rock, but confined to a humus layer. In my experience, it is a suboceanic species which is wholly lacking from calcareous sites.

Northward, the species is reported from moist granite, often on vertical siliceous walls, or in their crevices, or near margins of pools in granite, associated (east coast of Hudson Bay) with *Lophozia atlantica, L. kunzeana, L. wenzelii, L. ventricosa, Ptilidium ciliare, Scapania parvifolia, Cephalozia ambigua, bicuspidata* and *leucantha, Pleuroclada albescens* var. *islandica, Chandonanthus setiformis,* and *Gymnocolea inflata* (Schuster, 1951). In more oceanic sites, as in Newfoundland, commonly with *Cephalozia leucantha, C. media, Microlepidozia setacea, Lophozia attenuata, Bazzania trilobata, Lepidozia reptans,* and *Diplophyllum albicans,* and variously on moist or wet siliceous rocks, where often forming thick cushions, on wet soil, and occasionally on decaying logs (Buch and Tuomikoski, 1955). Very abundant in the New England mountains, as on Mt. Katahdin, where largely on moist rock-walls, large damp boulders and craggs, with *Anastrophyllum michauxii, Scapania umbrosa, Cephalozia bicuspidata, C. ambigua, Lophozia silvicola, Blepharostoma, Chandonanthus setiformis, Tritomaria quinquedentata, Lophozia atlantica,* and *Gymnomitrium concinnatum* (in drier than normal areas). Also over peat on banks, as at the bases of boulders, or on exposed, seepage-moistened, *Sphagnum*-covered ledges, or on sunny, peat-covered boulders, there with *Ptilidium ciliare, Lophozia attenuata, L. kunzeana, L. atlantica, Polytrichum,* etc.

Remaining frequent southward into the Catskill Mountains, where

forming swelling, spongy tufts on intermittently moist cliff-walls and crests, and there often with gemmae, occasionally perianths, rarely capsules; associated with *Anastrophyllum michauxii* and *Eremonotus minutus, Lophozia silvicola, L. attenuata, Bazzania trilobata, B. tricrenata, B. denudata, Diplophyllum taxifolium, Scapania nemorosa,* rarely *Calypogeia meylanii, Cephalozia media,* and *Lepidozia reptans.*

In Europe supposedly frequently invading peat bogs, a habitat more typical of the related *M. anomala.* I have never seen *M. taylori* from such sites, in North America. Inversely, *M. taylori* in eastern North America often produces gemmae, especially in the common, pigmented forms of rock walls. Schiffner (1910) has emphasized repeatedly the supposed rarity of such gemmiparous phases in Europe.

The plant usually is restricted to the Spruce-Fir Zone, but in Newfoundland occurs in "open tundra" near Quarry (*Fernald and Wiegand* 6448), associated there with *Lophozia* (*O.*) *kunzeanus.*

On dry cliff-crests the species often occurs long after pioneer conditions have passed, and then often is consociated with *Bazzania trilobata,* occasionally various Cladoniae.

Although typically epilithic, and occurring from pioneer to nearly climax conditions then, the species is often a transient element in the rapidly succeeding facies of the xylicolous *Nowellia-Jamesoniella* Associule. It apparently depends on a reservoir population on rocks, from which logs are invaded, since the species is quite lacking on decaying logs away from the montane habitats of the species on rock outcrops. On logs a wide variety of associated species occur, among them: *Cephalozia media, Lophozia porphyroleuca, L. incisa, Cephalozia leucantha, Bazzania trilobata, Anastrophyllum michauxii, Nowellia, Jamesoniella, Calypogeia suecica, Scapania umbrosa, Geocalyx graveolans,* etc.

Differentiation.—One of our easier Hepaticae to recognize in the field. The robust size, strong tendency for pigmentation (at least of the upper halves of the leaves) with a carmine to purplish to purplish-brown color (never the warm brown of the related *M. anomala!*) and nearly or quite orbicular leaves eliminate most species occurring in similar habitats. *Jamesoniella autumnalis,* which may occur with it, is only one-half the size, and therefore should not be confused with it, even in the field. It has much sparser rhizoids.

Under the microscope, the single, most salient diagnostic character is the very curious manner in which the cuticle of the leaves is adorned. The cuticle is coarsely roughened by what are almost irregular, jagged-appearing plates—giving the appearance of a smooth cuticle that has become irregularly fissured (Fig. 4:8). Frye and Clark (1943, p. 300) consider the cells of this species to be "verrucose"; this description is misleading. Gottsche, many years ago, aptly likened the cuticle of this species to an old plate, on which the glazed layer had cracked irregularly, forming polyhedral areolae. No other regional species has a similar cuticle. Sterile plants are also characterized by the fact that there are very distinct subulate to sublinear underleaves (usually largely hidden among the very characteristically abundant, dense rhizoids); by the large leaf-cells which

always bear bulging trigones, and by the strong tendency towards purplish-red to reddish-brown pigmentation. The plants, in my experience, are often gemmiparous, the gemmae being produced freely if not abundantly on the margins of the upper leaves. The leaves may become slightly longer with gemmae-production, but never attain the characteristically ovate-lanceolate form of the related *M. anomala.* Frye and Clark (1943, p. 300) confuse the leaf shapes of *M. anomala* and *M. taylori,* stating they are "usually ovate" above in the former, and "roundish to lanceolate" in the latter. The inverse, of course, is the case, *M. taylori* never producing lanceolate leaves. Fertile plants are frequent, especially on rock-walls, and the strongly laterally compressed perianths, inflated only towards the base, with a truncate mouth, at once eliminate most superficially similar species.

This species is so different in color, in the absence of ovate-lanceolate gemmiparous leaves, in the rough cuticle, and in the opaque, granular-appearing oil-bodies from the related *M. anomala,* that confusion between the two seems hardly possible. The restriction of the present species to rock-walls, and to logs near montane rock-outcrops, also separates it from the helophytic *M. anomala.* The oval to ellipsoidal oil-bodies, formed of numerous minute, little protruding spherules are very different from the few-segmented oil-bodies of *M. anomala.*

Other distinctions from *M. anomala* lie in the a) narrower, usually more subulate underleaves; b) the shortly ciliate perianth-mouth; c) the finely but slightly aerolate outer faces of the spores, which contrast strongly with those of *M. anomala,* where they are adorned with close, numerous, minute, short, vermiculate ridges or verrucae. The inner spore faces, in both species, are finely papillate. The capsule-wall in *M. taylori* varies, locally, from 3-4-stratose. Where three-stratose, the outer layer is 23-25 μ thick, the middle 8-10 μ, the inner, 10-12 μ; where four-stratose, the outer is 21-23 μ thick, the middle 5-6 μ, the inner 8-12 μ. The total thickness is usually 45-48 μ. The epidermal cells, where not irregular, average perhaps 23-28 μ wide x 50-75 μ long; they are adorned with thickenings that are extremely polymorphous, but nevertheless quite diagnostic, reminding one strongly of those of *Riccardia pinguis* in some respects. The nodular thickenings, which are largely confined to both longitudinal faces of alternating walls, appear somewhat stalked in profile, *i.e.,* their broadest part is well above the point of attachment to the radial longitudinal walls. The highly pigmented, distal, expanded portion of these thickenings is sometimes extended as a vague transverse band (then becoming incompletely semiannular), but more often the expanded portions of the thickenings are connected to each other by longitudinal, pigmented thickenings lying on the tangential walls some distance out from the radial walls, thus appearing to anastomose. In extreme cases a strong band is thus developed, lying just beyond the radial walls, along each side of the radial walls, which ties together the nodular thickenings into longitudinal rows. Similar thickenings of the

epidermal cells have been seen only in *Riccardia pinguis*. The innermost cell layer is equally distinctive in that the numerous, complete to subcomplete, tangential bands show an unusually high level of anastomosis with each other, the tangential bands occasionally merging, at other times being furcate into two or three slightly divergent bands that usually do not attain the opposite side of the cell. The inner cells average, where regular, *ca.* 23-28 μ wide x 75-120 μ wide; in some cases through subdivision, with occasional cells only 18-20 μ wide. The seta is *ca.* 540 μ in diameter, and has the epidermal cell rows slightly larger in diameter (1-1.5 × as large in diam.) as the inner cell rows; the epidermal cells average 55-60 μ in diameter. This contrasts considerably with the figure given in Müller (1911, fig. 343c), and his statement that the 18-20 rows of outer cells are twice the diameter of the inner ones.

Branching in *Mylia taylori* appears to be frequently terminal, except below the gynoecia. In one instance, terminal branching occurred at the apex of a shoot, which immediately produced on both main axis and branch perichaetial bracts, and then a perianth, resulting in closely approximated, gemminate gynoecia, each of which produced a single subfloral innovation. Subfloral innovations appear to be almost universally produced, and occur either singly or in pairs; they are apparently the only intercalary branches that are regularly produced.

Anomylia genus nova

Plantae filiformes, minutae; folia remota, obdeltoidia vel obcuneata, caduca; amphigastria triangularia vel lanceolata, patentia, permanentia; rhizoidia tantum ad basis amphigastriorum (interdum pauca ad basis foliorum); rami laterales et terminales; cellulae parvae, ca. 16-25 μ, trigonis distinctis; perianthium terminale, a latere compressum, ad os latum. Typus: *Jungermannia cuneifolia* Hooker.

Plants small or *minute, filiform, with remote, usually obcuneate caducous leaves;* growing in decumbent, intricate patches or as isolated, creeping stems. Stems slender, flexuous and rather *rigid, brittle,* the cortical cells 1-2.5 × as long as wide, *thick-walled, in 8-12 rows;* medullary cells thick-walled, few (3-8 rows), *slightly to somewhat smaller than cortical cells.* Leafy shoots generally less than 0.6 mm wide. Branching diffuse, monopodial, of the *Frullania*-type (lateral, replacing the ventral half of a lateral leaf) or sometimes ventral and from axils of underleaves. *Rhizoids few,* in small tufts, *confined to a restricted area at the bases of the underleaves,* rarely 1-2 from postical base of lateral leaves. Lateral leaves *remote and clearly alternate, usually obcuneate,* concave, inserted by a *very narrow* succubously oblique, nearly straight line of insertion, *freely caducous* (*the stems with age thus usually largely denuded*); leaf-margins entire, but leaf-apex subtruncate and *often somewhat retuse. Cells medium-sized, ca.* (12) 16-22 x 16-25 μ in leaf-middle, strongly collenchymatous usually, with distinct to bulging trigones; oil-bodies (in our species) formed of moderately discrete, numerous, slightly protuberant globules, thus papillose in form, ellipsoidal to subovoid, 2-3 (4-5) per

cell. Underleaves quite distinct, *lanceolate, undivided* (rarely lingulate and emarginate), *free from the alternate lateral leaves. Asexual reproduction only by means of caducous leaves.*

Dioecious. Female plants with terminal perianth, *laterally compressed, bilabiate at the wide mouth.* Capsule *subglobose* (*fide* Stephani, 1906, p. 219), its *wall bistratose; elaters equal in diameter to the spores. Monandrous.*

Genotype.—Jungermannia cuneifolia Hooker (= *Mylia cuneifolia*). Congeneric are the West Indian *M. antillana* Carr. and Spruce, and the South American *M. fragilis,* which are known to the author by description only. Herzog (1954, p. 38) expresses the opinion that these latter species are synonymous with "*Mylia cuneifolia.*"

Our only nearctic species is the ancient *A. cuneifolia,* a relict species of the ancient, early Tertiary flora, whose few relatives are of tropical affinity.

A small, isolated genus, differing from *Mylia* (s. str.) in the mode of asexual reproduction, in the form and number of oil-bodies per cell, in the much smaller cell size, the simpler stem-anatomy, leaf-form, and in the restriction of the rhizoids to the underleaf-bases. Differing from *Leptoscyphus* (to which possibly more nearly related) in the much smaller size, presence of caducous leaves, leaf-form, clearly alternate leaves that are not connate at base with the simple underleaves, and very simple stem anatomy.

The generic position of "*Mylia*" *cuneifolia* has long been disputed. Dumortier (1874) placed it in both *Aplozia* and *Coleochila,* genera which are not maintained today; Mitten (1851) first placed it in *Leptoscyphus,* which has often been included in *Mylia;* Stephani (1906) followed Mitten, but used the name *Leioscyphus cuneifolius;* Spruce (1885) placed the species in the genus *Clasmatocolea,* which is used today for a very different group of species; in 1889 Spruce then transferred the species to *Mylia,* in which it has been generally retained. Müller (1905-16, p. 793) states that the inclusion of the species in *Mylia* (= *Leptoscyphus*) appears to be "wenig natürlich."

In addition to not agreeing as to its generic position, the older workers at times did not regard the plant as a distinct species. For instance, Hübener held the plant to be delicate, young shoots of *Frullania tamarisci,* perhaps because of the nearly constant consociation with that species in Europe; Lindberg, by contrast, believed it to be the juvenile stage of *Plagiochila tridenticulata;* Bernet considered the species to represent juvenile plants of *Plagiochila asplenioides.* Hooker (1816) went so far as to state that the species was parasitic upon *Frullania tamarisci* — a view to which no credence can be lent today.

These divergent views as to the position and nature of the plant have led the author to restudy the species in detail. Although the collenchymatous cells, the relatively large oil-bodies (not unlike those of *Mylia taylori*), the discrete underleaves, and the (in related tropical species) laterally compressed perianth, suggest some affinity with *Mylia,* several characters speak strongly against such a generic assignation: 1) The specialized type of vegetative reproduction. As far as I am aware, all typical *Mylia* species, insofar as they reproduce vegetatively, do so by gemmae originating in fascicles from the leaf-margins

(as illustrated for *M. anomala*). Furthermore, in no natural genus with which I am acquainted do both gemmae-production (of the fasciculate type) and the development of caducous leaves occur. (*Radula,* which has both caducous-leaved species, and "gemmae"-producing species, produces only discoid gemmae!). Since the writer regards the various types of specialized asexual reproduction as of considerable age, hence significant, it would appear that this character eliminates *"M." cuneifolia* from *Mylia,* s. str. 2) The underleaves, in *"M." cuneifolia,* bear a restricted rhizoid-initial region at their base, much as in the Lejeuneaceae, in some Southbyaceae (*Arnellia*) and in the Lophocoleaceae, as well as in all families of the Ptilidioid-Lepidozioid-Calypogeioid developmental sequence. In the typical species of *Mylia* (*i.e.,* the gemmae-producing types), the rhizoids are numerous and occur all over the ventral merophytes and adjacent portions of the lateral merophytes, at least on mature plants, hence are not restricted to regions. Insofar as the writer is aware, the two types of rhizoid distribution are almost always (if not always) restricted to different genera or families.

For these two major reasons, as well as because of the entirely divergent facies of the species, the writer would suggest that *M. cuneifolia* (and its relatives) be separated from *Mylia,* s. str., generically.

I have spent many hours searching, in vain, for sex organs in the regional collections of *A. cuneifolia.* Evidently the local populations have lost the ability to develop archegonia and antheridia. Herzog (1954, p. 38), however, reports the species from Isla Magdalena, West Patagonia, where it occurs with perianths. Herzog states that the perianth corresponds exactly to that of the Guadaloupean *Anomylia antillanus* (C. et P.) comb. n. (= *Mylia antillana* Carrington and Pearson, Bull. Soc. Bot. de France 177, 1889), as pictured in the *Icones* of Stephani. He presumes that, possibly, these two species are identical with *Anomylia fragilis* (Jack et Steph.) comb. n. (= *Leioscyphus fragilis* Jack et Steph., Hedwigia 31 : 20, 1892), known only from Grenada and Mt. Roraima in northern South America.

Stephani (1906, p. 219) described the sporophyte of *A. antillana* as having a subglobose capsule, whose walls are bistratose and elaters equal in diameter to the spores. If this is truly the case, *Anomylia* is the only known genus of Plagiochilaceae with a bistratose capsule-wall. A 1:1 spore-elater diameter ratio would also serve to isolate the species of *Anomylia* from *Mylia* s. str. According to Stephani both *A. antillana* and *A. fragilis* are monandrous, with large and shortly pedicellate antheridia. This also contrasts to the normally 2-4-androus condition found in *Mylia.* If the observations of Stephani are correct, therefore, the genus *Anomylia* is sharply separable from *Mylia* and *Leptoscyphus* on both gametophytic and sporophytic bases.

Anomylia cuneifolia (Hook.) comb. nova

Jungermannia cuneifolia Hooker, Brit. Jungerm., pl. 64, 1816.
Mylia cuneifolia S. F. Gray, Nat. Arr. Brit. Pl. 1:694, 1821; Evans, The Bryol-

ogist 26:56, 1923; Müller, *in* Rabenhorst's Kryptogamenfl. Ed. 3, 6:885, fig. 313, 1956.

Leptoscyphus cuneifolius Mitten, London J. Bot. 3:358, 1851; Müller, *in* Rabenhorst's Kryptogamenfl. 6(1):792, 1911.

Aplozia cuneifolia Dumortier, Hep. Eur. 55, 1874.

Coleochila cuneifolia Dumortier, *Ibid.* 106, 1874.

Clasmatocolea cuneifolia Spruce, Trans. Bot. Soc. Edinburgh 15:440, 1885.

Leioscyphus cuneifolius Stephani, Sp. Hep. 3:18, 1906; Bull. Herb. Boissier, Ser. 2, 6:218, 1906.

Plants minute, usually in thin, interwoven small mats or patches, often as isolated creeping stems among other bryophytes, *filiform, reddish-brown* to (with age or when dry) even blackish-brown, the tip ends of the shoots characteristically *greenish or yellowish-green,* and contrasted to the mature portions of the plant. Leafy shoots *ca.* 300-450 μ wide to occasionally 650 μ wide, 2-8 mm long, irregularly curved to sinuous, rather *rigid and brittle* when dry, diffusely but freely monopodially branched; branches lateral or (*fide* Kaalaas, 1898) sometimes from axil of underleaves. [Evans (1923, p. 57) also states the stems "are mostly simple but occasionally give off one or more ventral intercalary branches from the axils of the underleaves." He does not mention the occurrence of lateral, terminal branches, but as is evident from Fig. 5 :2, 10, such branches certainly occur.] Rhizoids rather short, scarce, in *small tufts from bases of underleaves.* Stems *ca.* 45-65 (90) μ wide, the cortex of 8-12 rows of ± thick-walled cells averaging (17) 18-22 (24) μ wide x 20-30 μ long; medulla in 3 rows (branches) or up to 7-8 rows of cells (main stems), the cells somewhat to hardly smaller in diameter (13-17 μ) than the cortical cells, ± collenchymatous. Leaves inserted by a *short, slightly succubously oblique,* nearly straight line of insertion, *broadly ovate to obdeltoid,* 150 μ long x 140 μ broad to 220 μ long x 260 μ broad up to 270-285 μ long x 300-310 μ broad, distant, standing stiffly away from stem to squarrose, their distal width usually quite as great as their length or greater; apex rounded-truncate to subtruncate to truncate-retuse; leaves often slightly concave, *brittle and exceedingly fragile, easily caducous.* Median cells variable in size, often 12-16 x 16-20, at times 18-22 x 20-25 (27) μ, nearly isodiametric, collenchymatous and usually with rather thin to slightly thickened walls and distinct, large to bulging trigones; walls brownish, cuticle smooth; oil-bodies relatively small and few (2-3, occasionally 4-5) per cell, of small, little protuberant globules (appearing papillose but not segmented), rather transparent, colorless, *ca.* 4.5-6 μ to 4 x 5-6.5 μ up to 6 x 9 μ, ovoid to short-ellipsoidal or spherical. Underleaves polymorphic, distinct and relatively large, *ca.* 1/2 the leaf-length, 50-60 x 100-120 μ up to 90 x 170 μ long, lanceolate to ovate-triangular or cuneate to subulate, rarely shortly bilobed. Asexual reproduction via caducous leaves (and more rarely underleaves), the *mature stems largely or virtually entirely denuded* (see Schiffner, Oesterr. Bot. Zeitschr. 57:457, 1907).

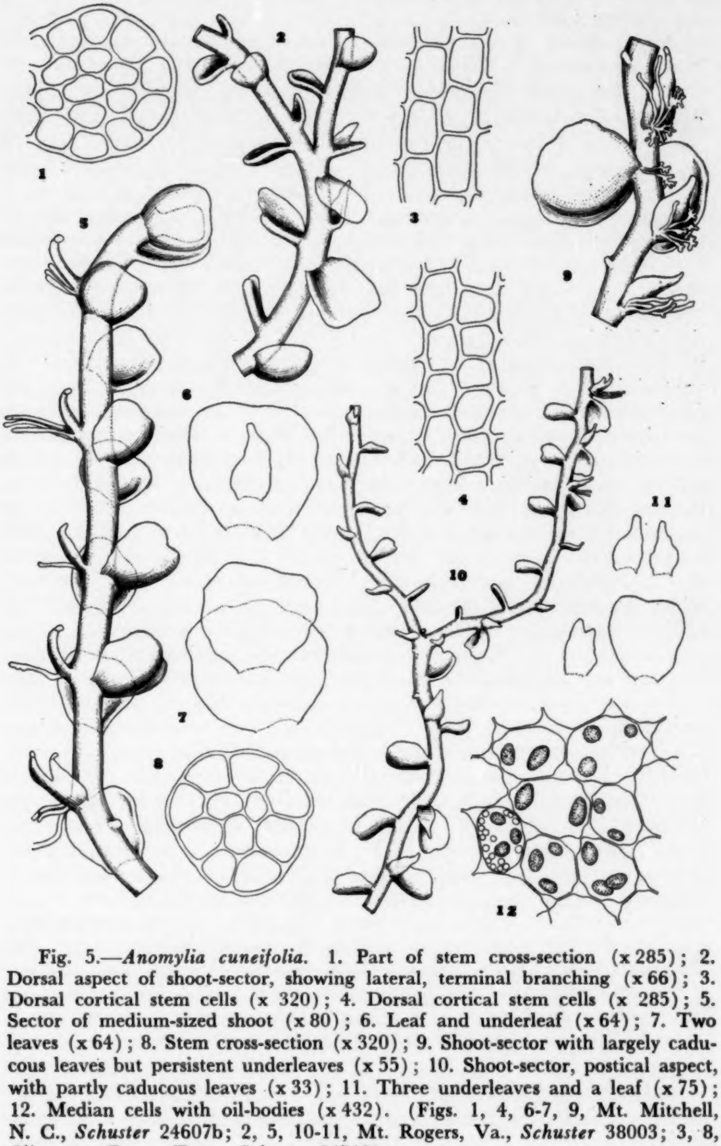

Fig. 5.—*Anomylia cuneifolia.* 1. Part of stem cross-section (x 285); 2. Dorsal aspect of shoot-sector, showing lateral, terminal branching (x 66); 3. Dorsal cortical stem cells (x 320); 4. Dorsal cortical stem cells (x 285); 5. Sector of medium-sized shoot (x 80); 6. Leaf and underleaf (x 64); 7. Two leaves (x 64); 8. Stem cross-section (x 320); 9. Shoot-sector with largely caducous leaves but persistent underleaves (x 55); 10. Shoot-sector, postical aspect, with partly caducous leaves (x 33); 11. Three underleaves and a leaf (x 75); 12. Median cells with oil-bodies (x 432). (Figs. 1, 4, 6-7, 9, Mt. Mitchell, N. C., *Schuster* 24607b; 2, 5, 10-11, Mt. Rogers, Va., *Schuster* 38003; 3, 8, Clingmans Dome, Tenn., *Schuster* 34712).

Sexual reproduction and organs unknown, in our population; but see Herzog (1954).

Type.—Bantry, Ireland (*Hutchins*). Schizotype fragment examined (from Mitten Herbarium) in NYBG.

Variation.—A stenotypic, ancient species, showing a limited amount of variation, depending partly on the substrate (bark or damp rocks), except for rather considerable variations in size. Relatively leptodermous modifications occur occasionally on rocks, but these appear to be totally lacking in North America where the species is exceedingly stenotypic and occurs largely on bark. The plants appear to occur invariably as a mod. *colorata-laxifolia-meso-vel pachyderma.*

Evans (1923) speaks of branching as ventral and axillary in this species, and states that the leaves are only 150-200 μ long and that "considerably smaller leaves are not infrequent." As is evident from the Virginian plants studied, branching is normally terminal and pseudodichotomous in this species, with the branch replacing the ventral half of a leaf. The supporting leaf is oblong to lingulate. In the American material studied, the slighter, more attenuate shoots may have leaves agreeing in size with those studied by Evans, but somewhat more robust branches, are not uncommon with leaves up to 310 μ wide x 285 μ long (Fig. 5:6-7). Similarly, Evans describes the underleaves as averaging about 100 x 50 μ, while in much of the material I have studied they attain a length of 170 μ x 90 μ broad. Kaalaas (1898), who has very carefully studied the species, states that although the underleaves and lateral leaves are free from each other, the two may at times be slightly adnate at base. Neither Evans (1923) nor the present writer have been able to confirm this.

Distribution.—An ancient oceanic species, restricted in occurrence to a few sites in Norway (Stavanger), Ireland, Scotland, in the latter regions locally not rare; also reported from the Azores (Allorge, 1950) and Madeira (Persson, 1939). In the New World only in the Southern Appalachian mountains at high elevations (4900 ft. and more; to 6800 ft.) in North Carolina and Tennessee, northward to Mt. Rogers in southwestern Virginia. Also reported from Tristan da Cunha and (Herzog, 1954) reported from Chile (Isla Magdalena, West Patagonia). The material reported by Herzog came from lava, and occurred sparsely, but with perianths! These have been previously unknown in this species. Herzog (p. 38) also makes the very interesting observation that *M. antillana* C. and M., from Guadeloupe, and *M. fragilis* (Jack et St.) from Grenada, are identical with *"M. cuneifolia."* He states that the perianth of the Chilean material of *M. cuneifolia* exactly corresponds to the drawing of that of *"Leioscyphus antillanus"* in Stephani's Icones.

Although exceedingly restricted in distribution, the species may be abundant in the "fog forests" of the Southern Appalachians, particularly in the dense, deeply shaded Fraser Fir forests, where it becomes an index species (of the corticolous *Bazzania nudicaulis-Herberta-Anomylia cuneifolia* Associule).

VIRGINIA: Mt. Rogers, *ca.* 5700 ft., Grayson Co. (*Schuster and Patterson* 38002, 38003, 38011, June 10, 1956). The northernmost report of the species from the New World (see Schuster and Patterson, 1957). NORTH CAROLINA: Mt. Mitchell (5711 ft.) and Mt. Pisgah (5649 ft.) (*P. O. Schallert* 5, 25, p.p.; *fide* Evans, 1923); Mt. Mitchell, Yancey Co., and Mt. Craig, both in Black Mts., 6400-6800 ft. (*Schuster* 23269c, 23268a, 23268, 23274, 23157, 23165a, 23167, 23165, 23165b, 23165c, 23275, 24607b, 23270); Andrews Bald and Clingmans Dome, *ca.* 6000-6500 ft., Swain Co. (*Schuster* 28117, 28112, 34714, 34715, etc.); Roan Mt., *ca.* 6100 ft., Mitchell Co. (*Schuster* 37698); Jones Knob near Balsam (*M. S. Taylor* 775!); Mt. Kephart (*Taylor* 2030!); Richland Balsam, on *Abies fraseri,* just E. and NW. of summit, 6250-6400 ft., in both Haywood and Jackson Cos. (*Schuster* 39698, p.p., with *Plagiochila tridenticulata;* 39645, 39687, etc.). TENNESSEE: Clingmans Dome, *ca.* 6500 ft., Sevier Co. (*Schuster* 34712, 34711a); Mt. Leconte, Sevier Co., *ca.* 4900 ft., above Alum Cave (*Schuster* 24100); Roan Mt., *ca.* 6100 ft., within 200 yards of N. C. state line, Carter Co. (*Schuster* 37731).

The distribution of this species very closely parallels that of *Cephaloziella* (*Cephaloziopsis*) *pearsoni,* an equally minute species, also almost exclusively confined to the bark of *Abies fraseri* in North America, and occasionally associated with *Anomylia cuneifolia.* The *Cephaloziella* occurs from southern Norway to England and Ireland, and recurs (Schuster, 1958a) from Roan Mt., Tenn.-N. C., to Clingmans Dome, N. C.-Tenn.

Occurrence.—In our region confined almost exclusively to the thin, flaky bark of *Abies fraseri,* at elevations of 4900 ft. or more, in the Great Smoky Mts., Black Mts., and adjoining ranges of the Southern Appalachians.

The species is nearly always corticolous in our area, and generally occurs as a pioneer on the regions of the trunk above the butt, usually associated with one or several of the following species: *Frullania asagrayana, Cephaloziella pearsoni, Lejeunea ulicina, Bazzania nudicaulis, Herberta sakuraii tenuis, Plagiochila tridenticulata.* The plant rarely forms pure tufts. Occasionally, at the lower zone of its occurrence, the more mesophytic corticoles that undergo ecesis on the butts of trees in the cool fog forests occur intermingled with it, among them *Tritomaria exsecta, Blepharostoma trichophyllum, Bazzania denudata, Anastrophyllum michauxii, Lophozia incisa, Radula tenax.*

The species, like the almost constantly consociated *Plagiochila tridenticulata,* also occurs on moist rocks in other portions of its range; it has been found in such sites, regionally, only once, on Roan Mt. (there associated with *Plagiochila tridenticulata, Metzgeria fruticulosa*).

Differentiation.—In the field the minute, brownish, decumbent, flexuous stems with minute, remote, shallowly-concave caducous leaves are quite distinctive. Under the hand lens, an extremely characteristic color-contrast is usually evident between the green apices of the shoots and the uniformly brownish mature parts of the plant. The plant differs from the slightly similar juvenile forms of *Bazzania nudicaulis* in the absence of any red in the brown pigmentation, in the much smaller size, and in the obviously truncate- retuse leaves with a narrow base.

Under the microscope, the distant, caducous, obcuneate, somewhat concave leaves, truncate-retuse distally, that possess a very narrow insertion, and the distinct underleaves easily characterize the species. The cells are small, as compared to *Mylia*: averaging at most 18-22 x 24-27 μ. Each cell bears 2-3, occasionally 4-5 oil-bodies, formed of discrete, somewhat bulging spherules. In the small size, and the few oil-bodies per cell, the species at once differs from our two species of *Mylia,* with which confusion is hardly possible. Macvicar (1926) shows the cells of this species as equally thick-walled; in type material from Bantry, Ireland (Miss Hutchins, *ex herb.* Hooker), as well as in all nearctic material I have studied, the cells are strongly collenchymatous, with more or less distinctly bulging trigones, as in our other species of the genus. The fragment of the type from Bantry (Mitten Herbarium, NYBG) which I have studied agrees completely with the material from the nearctic, at least as regards the vegetative organs; therefore, the conspecificity of the nearctic and palearctic populations can hardly be doubted.

PEDINOPHYLLUM Lindbg.

Plagiochila p.p., auctorum, incl. Dumort., Rec. d'Observ. 15, 1835 (p.p.).
Pedinophyllum Lindbg., Bot. Notiser 1874, p. 156 and Acta Soc. Sci. Fenn. 10:504, 1875.
Plagiochila subg. *Pedinophyllum* Lindbg., Not. Soc. f. fl. Fenn. 13:366, 1874.

Plants whitish-green to *pale green, growing decumbent,* forming *Chiloscyphus*-like mats. Stems *fleshy, freely monopodially branching, branches uniformly intercalary,* prostrate, *ca.* 330-370 μ wide x 260-300 μ high, *lacking differentiation into primary rhizomatous stems and secondary leafy stems,* in cross-section 9-12 cells high, the *cortical cells not differentiated from the medullary,* and not tangentially flattened (at best very slightly thick-walled, but not forming a sharp cortical region); dorsal cortical cells hardly narrower than leaf cells, hexagonal to short-rectangulate, little or not thick-walled, 22-27 (30) μ broad x 45-60 (70) μ long; *ventral 1-2 rows of cells becoming brownish and mycorrhizal.* Branches all intercalary and lateral, arising from the ventral half of the leaf-axils (upper half *fide* Müller, lower half in living material!) Rhizoids present to shoot-apices, *rather abundant, scattered over entire postical stem surface. Leaves alternate,* inserted by a *nearly straight,* not acroscopically arched (Fig. 6:3, 6) *oblique line of insertion* (*ca.* 35-45° to stem-apex), *not decurrent ventrally, very briefly decurrent dorsally;* leaves essentially rounded-rectangular, *flat or nearly so,* entire (occasionally emarginate with dorsal "lobe" often tooth-like and usually smaller; occasionally with small supplementary teeth); *antical convex fold absent or vestigial* (Fig. 6:4). Underleaves distinct, *small.* Cells *nearly isodiametric, delicate, thin-walled and virtually non-collenchymatous* (less often with distinct to barely bulging trigones); *oil-bodies fine-segmented,* ± *spherical, opaque and greyish, large,* 2-15 per cell. *Asexual reproduction absent.*

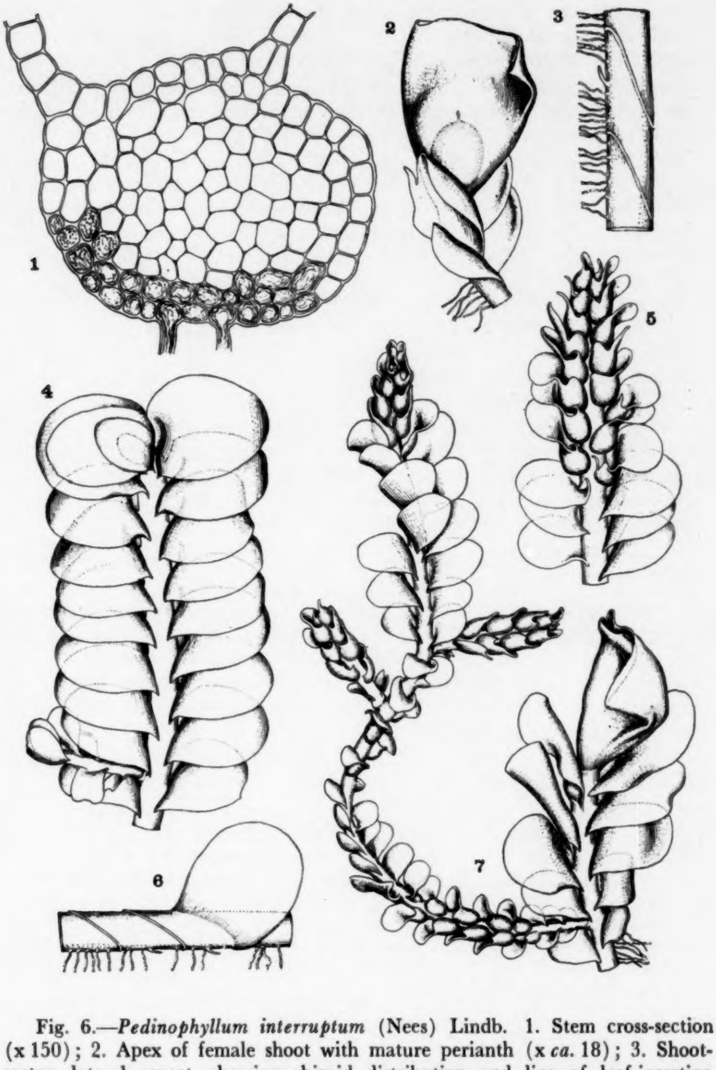

Fig. 6.—*Pedinophyllum interruptum* (Nees) Lindb. 1. Stem cross-section (x 150); 2. Apex of female shoot with mature perianth (x *ca.* 18); 3. Shoot-sector, lateral aspect, showing rhizoid distribution and line of leaf-insertion (x 25); 4. Shoot with immature female inflorescence at apex (x *ca.* 20); 5. Male shoot (x *ca.* 20); 6. Lateral view of leaf and shoot-sector (x 25). Fertile plant (x *ca.* 15). (All drawn from plants from Salisbury, Conn., *A. Lorenz*).

Autoecious.—Androecial branches arising variously from perianth-bearing shoots, or perianth-bearing shoot arising from androecial shoot (occasionally even from axil of perigonal bract). Perichaetial bracts similar to leaves (occasionally bilobed or somewhat dentate), larger than leaves; bracteole absent or small. Perianth laterally compressed, strongly so above, the *bilabiate apex broad and more or less truncate,* often deflexed to one side (as in *Plagiochila* spp.). *Androecia slender,* intercalary with age, of 4-8 pairs of loosely to somewhat imbricate bracts, smaller than surrounding vegetative leaves, the *dorsal base* (or a differentiated dorsal tooth or lobe) *ventricose and with margin incurved* to form an urn-shaped cavity; *antheridia single,* with a long, biseriate stalk. Capsule ovoid, longly pedicellate, wall 4-5-stratose; epidermal layer of large cells with nodular (radial) thickenings, the cells averaging 19-24 μ wide x 30-40 μ long, the thickenings prominent, evident (on careful focusing on free, external wall) as sparse nodular thickenings, but the nodular (radial) thickenings extending partly or largely across the tangential interior faces of the cells; interior layers with prominent complete to incomplete semiannular bands; innermost cell-layer with complete to incomplete semiannular bands, the cells irregular, mostly (10) 15-20 μ wide, elongate. Elaters not tapering perceptibly at the ends, 9-12 μ in diam., rather laxly bispiral, the brownish spirals 2.2-3 μ wide. Spores yellowish-brown, 12-15 μ, rather distinctly but not coarsely papillose.

Genotype.—*Plagiochila pyrenaica* Spruce (=*Pedinophyllum interruptum* var. *pyrenaicum*).

Habitually similar to *Chiloscyphus* (from which the smaller, undivided underleaves and smaller cells separate it when sterile, as well as—most simply—the scattered rhizoids) and to reduced, entire-leaved forms of *Plagiochila asplenioides* (from which the lack of differentiation of a cortex, the non-decurrent leaves and almost straight line of leaf-insertion separate it).

Differentiation.—*Pedinophyllum* differs from the other Plagiochilaceae in the autoecious inflorescence. Stephani describes a few autoecious species of *Plagiochila, P. autoica, P. monoica* and *interrupta.* The latter is here placed in *Pedinophyllum.* Carl (1931), pp. 35-36) states that "one must assume that both (of the other) species are not *Plagiochilas.*" Except for the inflorescence it falls very close to *Plagiochila,* from which it further differs in (1) the lack of differentiation into primary, rhizogenous stems from which arise the leafy stems (the shoots are leafy from the beginning, and rhizoidous to their apices); (2) the very slightly decurrent dorsal base of the leaf (in *Plagiochila* almost invariably more strongly decurrent, but see the notes under *Plagiochila columbiana* and *asplenioides*); (3) the absence of a convex "dorsal fold" of the leaf, with the dorsal leaf-margin nearly or quite flat; (4) the generally virtually non-collenchymatous cells (in *Plagiochila* more or less collenchymatous, but in a few species with the trigones virtually absent, and then as in

Pedinophyllum); (5) the subentire to sparingly dentate perianth-mouth, at best faintly denticulate (normally shortly ciliate to spinose-dentate or longly ciliate in *Plagiochila*); (6) the non-decurrent postical leaf-base with the line of insertion of the leaf scarcely arched (in *Plagiochila* almost invariably decurrent, usually quite distinctly so, with the line of insertion of the leaf thus more or less strongly acroscopically arched); (7) the virtual lack of a differentiated cortex (Fig. 6:1) (in *Plagiochila* with a distinct cortex, 2-5 cell-layers thick; without, as far as is known, a ventral mycorrhizal region, at least of the leafy stem).

The stem anatomy of *Pedinophyllum* closely approaches that of the Lophocoleaceae, and the genus might conceivably be regarded as derived from *Chiloscyphus*-like ancestral types. However, the scattered rhizoids and very much reduced underleaves argue against such a derivation, as does the perianth form. The possibility remains that *Pedinophyllum* is derived from the Lophocoleaceae by general narrowing of ventral merophytes, and the often therewith associated scattered distribution of the rhizoids.

Although the subentire, broad, laterally compressed mouth of the perianth, somewhat bilabiate at the apex, serves at once to identify *Pedinophyllum* as a relative of *Plagiochila* and *Mylia*, sterile material is very difficult to separate from other entire-leaved species with similar-sized cells (such as *Jamesoniella*). The total absence of pigmentation and more discrete underleaves, and absence of leaves that are emarginate with rounded lobes (such as occasionally are found in *Jamesoniella*) should separate it from the latter.

Confusion of sterile plants is very apt to occur with *P. asplenioides* forms (mod. *integrifolia-suborbicularis-parvifolia*). For instance, a specimen of *Plagiochila interrupta* (Venison Pickle, Labrador, Waghorne No. 1, Aug. 16, 1891; NYBG) is clearly *Plagiochila asplenioides*. The report (Burnham, on the basis of a determination by Conklin) of *Pedinophyllum* from the Lake George Region, New York (duplicate in author's collection) is also based on such entire-leaved forms of *P. asplenioides*. These forms differ from the *Pedinophyllum* as follows: (1) Leaves dorsally and ventrally at least somewhat decurrent; (2) cells with distinct trigones usually obvious (in the Waghorne material almost bulging); (3) leafy shoots with stem 15-17 cells high or more, with an obvious thick-walled, yellowish cortex 2-3 cells or more thick (in extreme mesic forms occasionally only 1-2 cells thick); (4) absence of mycorrhizae on leafy shoots (in *Pedinophyllum*, the ventral 1-2 cell layers of the stem brown and mycorrhizal).

Confusion between *Plagiochila* and *Pedinophyllum* has arisen because of the lack of understanding (at least in this country) of the extreme polymorphism which *Plagiochila asplenioides* exhibits. For instance, the most recent authors on North American Hepaticae (Frye and Clark, 1937-1947) confuse the entire-leaved forms of *Plagiochila asplenioides* with *Plagiochila arctica*, on one hand, and with *Pedinophyllum interruptum* on the other hand. (The descriptions of *P. arctica*, and illustrations, in that work are derived from a mod. *integrifolia* of *P. asplenioides;* at least one of the three "Examinations" they report of *Pedinophyllum* also represents such an entire-leaved modification of *P. asplenioides*.) It must be recalled that, under unfavorable conditions, *P.*

asplenioides may show no trace of the usual differentiation into an appressed, reduced-leaved rhizogenous rhizome-like primary stem-system, and a secondary, more or less ascending, nearly or quite rhizoid-free leafy-shoot system. Indeed, the stems may be unbranched, leafy, and decumbent throughout and the leaves may fail to develop marginal teeth. The leaf-shape itself is subject to modification: instead of becoming ovate, with the greatest width immediately above the base, and with strongly decurrent dorsal "fold," the leaves become broadly ellipsoidal to rectangular-rounded in shape, may be retuse distally, and show only slightly arched (hence nearly subparallel) antical and postical margins, with the greatest width of the leaf near its median point. Such leaves also are scarcely decurrent ventrally, shortly decurrent dorsally, and show the convex antical "fold" to a relatively slight degree, compared with the optimal manifestations of the species. However, even such persistently "juvenile" forms of *P. asplenioides* show a stem 14-16 cells high, with at least a distinct unistratose cortex (of smaller, more or less thick-walled, flattened cells), and usually with the cortex at least bistratose. Furthermore, the leaf-insertion is more distinctly arched (compare Figs. 6:3 and 8:1), and the leaves show at least a trace of the "convex basal fold" of the antical margin. In drying, the deflexed antical leaf-margin tends to become even more strongly bent under, and the characteristic leaf-form of *Plagiochila* is more readily evident. By contrast, *Pedinophyllum* in drying, has the leaves almost plane — exactly as they are when moist. In extreme cases, therefore, the habitual differences between the plants, and the stem-anatomy, must be used for identification.

PEDINOPHYLLUM INTERRUPTUM (Nees.) Lindbg.
Figs. 6-7:1-8

Jungermannia interrupta Nees, Naturg. Eur. Leberm. 1:165, 1833.
Plagiochila interrupta Dumort., Rec. d'Obs. 15, 1835.
Jungermannia dumortieri Libert, Pl. Crypt. Ardennes 4:311, 1837.
Plagiochila pyrenaica Spruce, Trans. Bot. Soc. Edinburgh 3:200, 1842.
Plagiochila macrostoma Sullivant, Musci Alleg. No. 221, 1846.
Pedinophyllum interruptum (Nees) Lindbg., Bot. Not. 156, 1874; Pearson, Hep. Brit. Isl. 269, pl. 111, 1900-1902; Evans, Rhodora 12:200, 1910.
Plagiochila microstoma Sullivant, *in* Frye and Clark, Univ. Wash. Publ. Biol. 6:269, 1937-1947.
Plagiochila interrupta var. *pyrenaica* Lindberg, *in* Hartman, Skand. Fl. 130, 1871.
Plagiochila (*Pedinophyllum*) *pyrenaica* var. *interrupta Lindberg,* Not. Fauna Fl. Fennica 13:367, 1874.
Leptoscyphus interruptus Lindberg, Musci scand. 4, 1879.
Plagiochila (?) *lobata* Kaalaas, Nyt. Mag. f. Naturv. 33:274, 1893.
Pedinophyllum pyrenaicum var. *interruptum* Schiffn., *in* Engler & Prantl, Nat. Pfl.-Fam. 1(3):89, 1893.
Pedinophyllum pyrenaicum Lindberg, Acta Soc. Sci. Fenn. 10:504, 1875; Buch, *in* Buch, Evans & Verdoorn, Ann. Bryol. 10:4, 1937.

The various Stephani species, *Clasmatocolea truncata, P. integra, P. laevicalyx,* placed by Hattori (1950, etc.) in synonymy under *P. interruptum* are not assigned to synonymy under this species here because there is still some question as to whether one or the other of them may not prove at least subspecifically distinct. (Since this was written, Inoue, 1958, has separated the Japanese plant as a subspecies *truncatum.*)

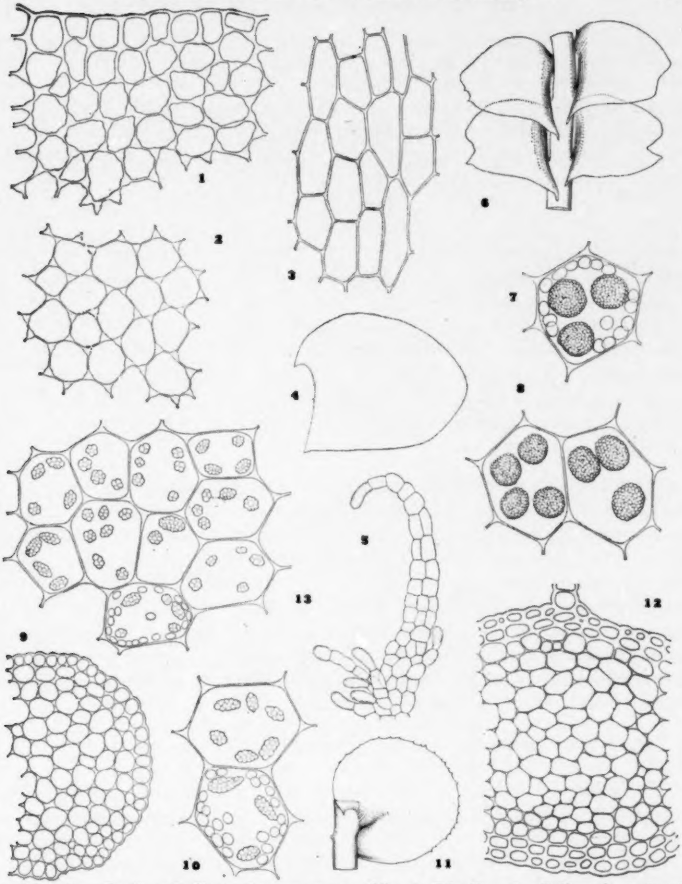

Fig. 7.—*Pedinophyllum interruptum* (Nees) Lindb. 1. Cells of perianth-mouth (x 185); 2. Median leaf cells (x 185); 3. Dorsal cortical cells (x 185); 4. Leaf (x 18.5); 5. Underleaf (x 105); 6. Part of shoot of var. *pyrenaicum* (x 12); 7-8. Cells with oil-bodies of var. *pyrenaicum* (7, x 515; 8, x 455). *Plagiochila asplenioides* (L.) Dum. 9. Half of seta cross-section (x 95); 10. Median cells (x 400); 11. Leaf, postical view, *in situ* (x 9.5); 12. Stem cross-section of the mod. *integrifolia* from Labrador, cited in the literature as *"Pedinophyllum"* (x 140); 13. Median cells with oil-bodies (x 342). Figs. 1-5 from plants from Salisbury, Conn., *A. Lorenz;* 6, from France, Schiffner's Hep. Eur. Exsic. No. 241; 7-8, from English plants, leg. *Appleyard;* 9, Tennessee, *Schuster* 34645; 10-11, Calander, Pertshire, England, *Jones;* 12, Labrador, *Waghorne*, a mod. *integrifolia* forming the basis for literature reports of *Pedinophyllum* from Labrador; 13, Turkey Run State Park, Ind., *Schuster* 18337, a juvenile plant superficially identical with *Pedinophyllum i. pyrenaicum* in fig. 6).

Plants usually in thin, flat patches, *usually over calcareous rocks,* yellowish-green to green. Stem soft, greenish, 275-300 (370) μ in diam. Shoots with leaves *ca.* 2-3 (4) mm wide, rather freely monopodially branched. Leaves contiguous, spreading laterally, *usually nearly flat* or weakly convex, sometimes somewhat erect-spreading, *rounded, short-rectangular to broadly elliptical-rectangular,* averaging ca. 800 μ wide x 820-900 μ long to 860-920 (1350) μ wide x 1050-1150 (1500) μ long. Underleaves minute and inconspicuous, filiform to lanceolate, usually discrete only on younger stems (and there often not always developed). *Cells thin-walled, ca.* 20 μ on margins, 20-25 x 25-35 μ in the leaf-middle, near base little more elongate; cell-walls very thin, the *trigones virtually absent to small;* oil-bodies (from European material) relatively large, granular to hyaline, mostly elongate-ovate, 3-8 per cell, 5-7 x 9-10 μ, formed of numerous small (*ca.* 1 μ) to relatively large (*ca.* 2 μ) globules that protrude through the surface membrane, hence *finely segmented in appearance;* cuticle smooth.

Androecia becoming intercalary, of 4-5, occasionally 7-8 pairs of imbricate bracts that are smaller than normal vegetative leaves; bracts very strongly saccate at the antical base, with the margin incurved, and provided (some distance above base) with a sharp, sometimes incurved tooth; apices of bracts entire, unlobed. Female bracts like leaves (but with a slightly greater tendency to be remotely dentate than vegetative leaves), larger than leaves. Perianth strongly laterally compressed above, the *bilabiate apex very wide, squarely truncate,* the mouth entire to (var. *pyrenaica*) finely denticulate or dentate. Spores 12-15 μ; elaters *ca.* 9-12 μ wide.

Type.—Basel, Switzerland (*Nees,* frère) 1813.

Variation.—Pedinophyllum interruptum represents an ancient species with a very puzzling distribution. It is widespread, and at times common, in central and northern Europe, appears widespread in Japan, and occurs in eastern North America from Greenland (?) southward to Connecticut and Ohio. The species appears to consist of two or more races. The Japanese material, listed by Hattori (1951a, p. 77) as *Pedinophyllum pyrenaicum,* has more numerous oil-bodies, occurring 15-25 per cell, with each *ca.* 6 x 7-13 μ or 5-5 x 10 μ. Unfortunately, the oil-bodies of the North American population are still unknown. The European material consists of two evidently genetically discrete extremes, an entire leaved form (typical *interruptum*), and a form with the leaves with a few teeth (usually 2-3 confined to near apex), the bracts more dentate usually, and the perianth-mouth denticulate to copiously spinose-dentate; the latter represents the var. *pyrenaicum*. Although this is possibly merely a luxurious form (it often is larger than the typical material, becoming at times 4-5 mm wide), it probably represents a considerably different genotype. At

one time it was considered a discrete species, but today all workers agree in that it represents merely a distinct variety. It does not occur in North America.

The nearctic collections are very few, and morphologically all belong to typical *interrupta*. Kaalaas described (De distrib. Hep. in Norvegia, 274, 1893) a *Plagiochila* (?) *lobata*, which both Stephani (Spec. Hep. 2:316) and Müller (1911:779) place in *P. interruptum*. Joergensen (1934, p. 173), however, places it in *Plagiochila*. This appears to represent an extreme form, of the size of var. *pyrenaica* with the leaves divided to ¼-½, with the postical lobe large and usually obtuse to narrowly rounded. It has the antical margin often reflexed (thus approaching *Plagiochila* in facies), and the postical margin occasionally with a few fine teeth. This variant has also not been found in our region.

The varieties *pyrenaica* (Spruce) Lindberg, and *lobata* (Kaalaas) K. M. (in Rabenhorst's Kryptogamenfl. 6(1):779, 1911) serve as a vivid demonstration of the distinct relationship of the genus to *Plagiochila*.

Range.—An exceedingly rare species in North America, of very sporadic occurrence. In our region limited to the Deciduous Forest Region from Massachusetts to Connecticut, west to Ohio; certainly to be found with a wider distribution.

MASSACHUSETTS: "On sandy ground (along rivulets?) Ipswich" (*Oakes*); CONNECTICUT: "In shaded glen back of old limestone quarry east of Lakeville," Salisbury, 725 feet (*Lorenz, June 13, 1916!*) (NYBG; a duplicate of the Lorenz material, in the NYBG has been used in the preparation of the illustrations); "On dolomite rocks in a ravine, Brookfield" (*Evans, 1910*). OHIO: "On old logs, Cat-tail marsh," near Urbana (*Sullivant!;* type of *P. macrostoma*); on limestone along Cedar Creek, near Beaver Pond, Adams Co. (*M. S. Taylor 121!*); on ground among mosses, Cedar Swamp, Champaign Co. (*M. S. Taylor 56!*); on logs below dolomite cliffs, creek near Beaver Pond, Adams Co. (*M. Fulford, 1930!*).

Also reported from NEW YORK (Washington Co., *Burnham*); Frye and Clark list the species under their "Examinations" from here; I have examined Burnham's material and find it to represent the entire-margined form of *Plagiochila asplenioides*. I have also studied a specimen of "*Pedinophyllum interruptum*" from Little Moose Lake, Herkimer Co., New York (*Haynes* 916); this is typical *Chiloscyphus polyanthus*. Also reported (Macoun, 1902, Frye and Clark, 1943) from Labrador; the only specimen so labelled that I have seen (Waghorne No. 1, "Venison Pickle," Aug. 16, 1891, NYBG) is clearly *Plagiochila asplenioides*, as is evident from the stem anatomy, the leaf-insertion, and the very evident trigones. The other reports of the species in Frye and Clark (Ontario; Illinois) are equally ambiguous, and should not be accepted without study of the material in question. However, the report of the species from Greenland may be valid. The reports from British Columbia (Frye and Clark, p. 271, based on Macoun, 1902) are also erroneous; I have examined a specimen of Macoun's Canadian Hepaticae No. 121 (In wet places, in woods, Albert Canyon, Selkirk Mountains, B. C., May 29, 1890; and Gold Range, B. C., 1889); this is clearly a mod. *integrifolia-leptoderma* of *Plagiochila asplenioides*,

in which the stem is 15-16 cells high, with the 2-layered cortical, small cells not strongly thick-walled; however, the strong development of the convex basal fold of the leaves, and the strongly deflexed antical leaf-margin clearly place the plant in *Plagiochila*. I have not been able to check the report from Alberta (Brinkman, 1934), but cannot accept it until actual material is verified.

Ecology.—Wholly restricted to calcareous sites. The species has been very rarely collected in North America, more frequently, perhaps, by Mrs. Mary S. Taylor than anyone else. She writes that her material (from Ohio) is "from limestone areas and growing with Arbor Vitae." Indeed, the species appears to be frequent in our area in Cedar (*Thuja*) swamps, where it grows on the ground, among mosses, on logs below dolomite ledges, or on limestone along creeks, such as along Cedar Creek, Adams Co., Ohio, or on dolomitic rocks. The species is a distinct mesophyte. Unfortunately, from the viewpoint of recognition of the plant, *Plagiochila asplenioides* is often found in similar sites. Other associates, locally, are *Mnium* spp. and, when the *Pedinophyllum* occurs on logs, *Cololejeunea biddlecomiae*.

Differentiation.—Although the plant has been widely confused in this country with *Plagiochila asplenioides,* it is habitually quite unlike this, resembling more closely *Chiloscyphus pallescens* in facies: particularly in the rather pellucid, whitish-green color, the rounded-oblong leaves that average slightly longer than broad, and which are laterally patent (and little, or not convex in most cases). As Evans (1910) points out, the two taxa also agree in the abbreviated female branch, although in *Pedinophyllum* it "is never quite so abbreviated as in *Chiloscyphus* and may bear several pairs of leaves." This is also clearly the case from Figure 6. When sterile material is at hand (and this appears to be rarelv the case in *Pedinophyllum*), the much smaller underleaves, the relatively small cells with small trigones, and the numerous rhizoids serve easily to identify the *Pedinophyllum*. In the latter the rhizoids are freely scattered, and not restricted to the underleaf-bases as in *Chiloscyphus*. Furthermore, the perianths are broadly truncate at the mouth and laterally compressed, and the androecia are narrower, with the bracts much smaller than leaves, more erect. As Evans has pointed out, the perigonal bracts of *P. interruptum* "bear a small pouch or lobe at the antical base, agreeing closely in this respect with *Chiloscyphus*." However, the distal portion of the bracts are leaf-like and elaborated in *Chiloscyphus,* usually quite reduced in *Pedinophyllum*. In fresh condition, the few and very large oil-bodies of *Pedinophyllum* will at once separate it from *Chiloscyphus,* in which the oil-bodies never appear to virtually fill the cell-lumen.

The various manuals stress, as one of the distinguishing features of *Pedinophyllum,* the very leptodermous cells. At least in some of the plants from Ohio the cells of the leaves, and even more so the cells of the distal portions of the perianth, are quite strongly collenchymatous. In all of our plants the perianths are vertically truncate at the mouth, with the truncation never showing any tendency towards production of teeth.

PLAGIOCHILA Dumort.

Martinellia sect. *b* Gray, Nat. Arr. Brit. Pl. 1:692, 1821.
Radula sect. *Plagiochila* Dumort., Syll. Jungerm., 42, 1831.
Plagiochila Dumort., Rec. d'Observ., 14, 1835 (p. max. p., not incl. *P. interrupta* Nees); Carl, Ann. Bryol., Suppl. Vol. II:38, 1931 (except subgenus *Oppositae*).

Plants medium sized to very robust, commonly 1.5-8 mm wide, normally with at least sparing, intercalary branches from the lower ends of the axils of the leaves, *never or only sporadically* (and abnormally?) *with postical intercalary branches;* in addition, usually with terminal branches of the *Frullania*-type present (and sometimes almost exclusively branching thus), and often with subfloral innovations on one or both sides; *without postical stolons.* Shoots usually dimorphic: *a basal, creeping, small-leaved rhizomatous primary stem system,* usually freely rhizoid-bearing, usually developed (rarely vestigial), *from which arise the variously ramified* (or rarely unramified) *aerial, leafy shoots, which are usually nearly or quite without rhizoids.* Stems somewhat oval in cross-section, usually somewhat brownish, rarely green, *firm, and rather rigid,* rarely soft, the aerial usually ascending or loosely procumbent, usually rather slender; cortical cells rectangulate, somewhat to strongly *thick-walled, usually strongly elongated, in* (1) 2-4 (5-6) *strata, tangentially more or less flattened,* somewhat to considerably *smaller than medullary,* which are strongly elongated, pellucid, thin-walled; mycorrhizal infection nearly or quite absent. *Rhizoids, where present, scattered,* colorless. *Leaves clearly alternate, free from each other* both antically and postically, inserted by an acroscopically arched insertion (*thus decurrent both antically and postically,* often longly so), *clearly succubously inserted* and oriented, very varying in shape and dimensions, but *usually variously armed with marginal teeth, cilia, spines, or lobes,* rarely entire or subentire (in modifications of species that otherwise are dentate-leaved); *antical margin reflexed, often strongly so,* forming a convex antical fold, or cnemis. *Underleaves always present, although often reduced* to 1-several uniseriate short ciliary segments, frequently the divisions *ending in longly clavate slime papillae,* with maturity often obsolete and disappearing. Cells collenchymatous, often strongly so, small to large (13-40 μ wide usually, in leaf-middle), each cell with several (usually 4-15) homogeneous, coarsely segmented, or rarely finely granular segmented *oil-bodies, small to moderate in size* (less than half the cell-length). Asexual reproduction often present, various (caducous leaves, leaf-lobes or fragments, propagula from the leaf surface, etc.), but *never by means of fasciculate gemmae.*

Always dioecious; rarely producing sporophytes. Androecia usually *compactly spicate, and much narrower* than vegetative portions of shoots, the $\pm$ imbricate *bracts smaller than leaves,* strongly ventricose and erect, except for the spreading to squarrose apices; bract margins toothed like leaves, but often less strongly so, frequently

entire; androecia on leading branches and then *usually becoming intercalary,* or on short, often fasciculate lateral or terminal branches (and then usually remaining terminal); antheridia usually 2-3 (but ranging from 1-10), the *stalk biseriate.* Gynoecia variously terminal on leading or ultimate, abbreviated leafy stems, *often with 1-2 subfloral innovations,* bracts usually in one pair; bracts generally hardly differentiated from leaves, rarely much larger in size, but the margins usually more sharply toothed, often concave at base and somewhat sheathing, but erect-spreading to widely spreading distally, the antical margins more often with scattered teeth, usually sharply reflexed; bracteole absent or vestigial. Perianth various, always more or less inflated below, *strongly laterally compressed above, wide and usually obliquely truncate at the mouth,* often sharply keeled antically (less often also to some extent postically). *Perigynium absent;* calyptra free, with sterile archegonia confined to base. Seta of numerous cell-rows, the *epidermal not larger than inner, often quite short.* Capsule ovoid-subglobose, firm, 4-valved to base, the wall usually 4-7 (8) cell-layers thick. Elaters 2-spiral. Spores *ca.* twice the elater diameter, finely granulose.

Genotype.—Plagiochila asplenioides (L.) Dumort.

The above diagnosis has been prepared to sharply separate out the recently segregated genera *Chiastocaulon, Plagiochilion* and *Plagiochilidium.*

* * *

There has been no review of the nearctic species of the genus *Plagiochila* since that of Evans (1896), excepting the compilation of Frye and Clark (1944). Since the paper by Evans is now much out of date, and was amplified and modified by that author subsequently (1905, 1914), a revision of the genus, as it occurs in our area, is much needed. This is particularly the case since it is impossible to use the key in Frye and Clark (1944). Although these authors saw material of 13 out of the 15 species they treat, they examined the type material of only 3 out of the 15 species, and of the remaining species studied, saw only a single specimen each of 4 of these species. It seems scarcely possible to form any understanding of a genus as complex and polymorphic as *Plagiochila* from such a study. The present taxonomic treatment differs considerably in reducing *P. fryei* to a synonym of *P. alaskana,* and the latter in turn to a synonym of *P. semidecurrens grossidens; P. crispata* to a subspecies of *P. undata; P. smallii* to a synonym of *P. diffusa,* and in the treatment of *P. arctica,* which, as is evident from the remarks of Persson, and the description and figures of Frye and Clark, was quite misunderstood by these latter authors. The writer has seen type material of all of the New World endemics which have been described from North American material, as well as of *P. diffusa* (described from Cuba); it is only of the 3 more widespread species (*P. asplenioides, tridenticulata, arctica*) of which types have not been seen. With the present status of knowledge of the

genus *Plagiochila,* it was believed a major service to the student of the group would be rendered by preparing detailed illustrations of the species *from type material.* Insofar as living material could be collected, drawings of the cells have also been prepared to show the oil-bodies and chloroplasts.

Early in the present study it was found that the species of the genus occurring within our borders are much more sharply definable than one would gather in the treatment of Frye and Clark. In fact, utilizing their key, much material of many of the species is not determinable. For instance, these authors separate *P. austini* from *floridana* on the basis of "Leaves not decurrent ventrally" vs. "Leaves decurrent ventrally." A glance at Figure 29:2 and Figure 54:1 clearly indicates it is impossible to separate the two on that basis. Again, most of the common forms of *P. asplenioides* are edentate, and would key to *P. arctica* in the key of Frye and Clark. In fact, the figures and description of *P. arctica* in Frye and Clark are based on a specimen of *P. asplenioides.* The size of the plant is used (and quite erroneously) to separate *P. austini* from *P. virginica,* supplemented by a fancied difference in whether the underleaves are present or absent. Since these differences do not exist, the considerably different *P. austini* and *virginica* are quite confused in that treatment. *P. undata* is supposed (p. 435) to have the leaves strongly undulate on the dorsal margin, whereas only the ventral margin is undulate. Thirteen species of *Plagiochila* are separated from *P. tridenticulata* as with "Most of the leaves not 2-lobed or if so the lobes again irregularly lobed." Unfortunately, forms of *P. austini* (Fig. 30) would also be sought under this heading.

Twenty-three species are here reported from North America, north of Mexico, together with seven varieties. Two of the species, three subspecies, and seven varieties are described as new. This represents a considerable increase in the number of species previously reported (fourteen, allowing for the synonymy of *P. fryei,* listed by Frye and Clark [1944] 1945).

TAXONOMY

Plagiochila, with between 1200 and 1300 described "species" is the most difficult and by far the largest genus of the Hepaticae. The size of the genus is not the sole nor major source of difficulty. It is the extreme polymorphism of the vast majority of species that is responsible for the chaotic taxonomy of the genus *Plagiochila.* To a slight degree, the existing confusion has been lightened by the separation of three "genera" from *Plagiochila, Plagiochilidium* Herzog, *Chiastocaulon* Carl, and *Plagiochilion* Hattori—the latter founded for the opposite-leaved species. There remain in the genus only the alternate-leaved species to be considered—which still include over 99% of the species formerly placed in the portmanteau genus *Plagiochila.* The estimated 1200-1300 species left in *Plagiochila* are founded largely on the characters of 1) leaf-form and orientation; 2) underleaf size and form; 3) cell size and mode of thickening of the wall; 4) nature of the armature of the leaf. The reliance on vegetative characters is necessary, unfortunately, since in only a minority of species do we know the perianth, and in only exceptional cases, the sporophyte. In

fact, of the relatively well-known nearctic species, the sporophyte is known only for *P. asplenioides*. The exceedingly unsatisfactory status of the taxonomy of the genus, based on the above characters, is partly due to the prevailing dioecious nature of the species (and often habitual sterility). Only a very few autoecious species are described and Carl (1931) doubts their belonging in *Plagiochila*. When one recalls the recognized polymorphism in such a well-known species as *Plagiochila asplenioides*, and considers the fact that of hundreds of "species" of *Plagiochila* only the type specimen is known, the conclusion that the genus is "over-inflated" becomes inescapable. To what degree some of our relatively few species will prove to be subspecies of more widely distributed types is impossible to predict at present.

The integration of the species of *Plagiochila* has, in the writer's opinion, been furthered only to a limited degree by the study by Carl (1931). Carl states that in the taxonomy of the genus "Der geographische Gesichtpunkt ist unbedingt zu verwenden. Er gibt ein erstes leicht zu definierendes Einteilungskriterium ab. Erst die weitere Gliederung ergibt sich aus der Morphologie der Pflanze. Als Beleg für die Brauchbarkeit einer geographischen Einteilung mag erwähnt sein, dass wir z. B. keine einzige paläotropische Art aus America kennen." With such an emphasis on the geographical distribution, the point is attained where the single most important criterion not only of the species, but of the species group, is its distribution. If we take species such as *Plagiochila tridenticulata* (Azores, Ireland, England, France, the Southern Appalachians) and *Plagiochila asplenioides* (holarctic) the "geographical point of view," as used by Carl, becomes impossible to defend. By using the "geographical point of view," such related species as the "Atlantic" European *Plagiochila spinulosa* and *ambagiosa* and the Southern Appalachian endemic *P. sharpii* become separated so far "phylogenetically" that their understanding becomes quite impossible. These species, and the western American "*P. alaskana*," are related to the East Asiatic *P. semidecurrens* (pp. 4-5). The latter, Carl places in the Sectio Zonatae, which is supposedly restricted to the Paleotropics. Alaska is hardly in the Paleotropics. It would appear, to the writer, that a complex of species, showing an origin from a common, ancient, hyperoceanic ancestor can be assumed; *P. spinulosa* and *ambagiosa* are oceanic species of the warmer parts of western Europe. *P. sharpii* is an endemic of the *Hymenophyllum tunbridgense* region of North America (much as *P. spinulosa* is common in the *H. tunbridgense* areas of the oceanic region of Europe), and is oceanic in affinity. "*P. alaskana*" occurs on the hyperoceanic Alaskan coast (where such oceanic elements as *Pleurozia purpurea* occur — a species again found in the Himalayas, the oceanic portions of Europe, with related species in Japan). *P. semidecurrens* occurs in Japan, and eastern Asia, to Yunan. This collective pre-Tertiary distribution pattern is not novel to this species group. With the recognition of such distribution modes, the basic division by Carl becomes increasingly difficult to utilize.

Fortunately for American students, the nearctic *Plagiochila*-flora is much less diversified than that of the Neotropics, and only a few neotropical species have been able to penetrate into our region. For that reason, the numerous problems which Carl had to cope with in his world treatment of the genus, and which he has in many instances

admirably resolved, have not been of insurmountable difficulty, and it has been possible to use, with only minor modifications, most of the sections suggested by Carl (1931). It must be emphasized that the writer has placed much more emphasis on three criteria of probably very great significance (mode of asexual reproduction, branching, and nature of the oil-bodies), which were not sufficiently emphasized in the work by Carl, or were omitted. Utilizing these concepts, the following synopsis of our sections may be derived:

A CONSPECTUS OF THE SECTIONS OF NEARCTIC PLAGIOCHILA

1. Plants with a discrete basal vitta of elongate cells (*ca.* 14-20 (24) x 40-52 μ); leaf-cells unusually small, 14-18 (20) μ wide near leaf-apex and leaf-middle, strongly collenchymatous and with bulging trigones (even at sites with low saturation deficit); freely producing sex organs, but devoid of any mode of asexual reproduction; leaves ovate-triangular to ovate-orbicular, widest slightly above base, rather short (length 1.0-1.5 the supra-basal width), strongly postically secund, the margins uniformly dentate, the teeth numerous, ± regular (usually 12-40 per leaf); oil-bodies numerous, small, homogeneous; plants shiny when dry, developing a brownish pigmentation; branching exclusively intercalary, monopodial; perianth elongated, long-exserted, the keels much longer than the width of mouth. ....Sectio ZONATAE (*P. sharpii, semidecurrens*)

1. Plants without a vitta, the basal cells averaging over 20 μ wide and less than 2-2.5 × as long as wide; apical and median cells usually 19-38 μ wide; leaves not or weakly postically secund, with few and coarser marginal teeth (or plants able to develop entire-leaved modifications); oil-bodies segmented (or reproducing only by caducous leaves or leaf-lobes). 2

   2. Plants reproducing readily by caducous leaves (which never develop leafy propagula before dehiscence) or leaf-lobes or fragments; leaves remote to contiguous, narrow at base, parallel-sided or widest at or above middle, narrowly inserted, not or very short-decurrent, both postically and antically, rectangular to obovate or obdeltoid in outline; leaves usually with a sharp tendency to be bilobed (the lobes often again toothed or lobed); cells ± strongly collenchymatous (even under low saturation deficit); brownish with age, often glistening; branching exclusively intercalary. Plants rarely reproducing sexually, never by leafy propagula; small (0.5-1.5 mm wide) to medium-sized (1.25-2.5 [3.2] mm wide). 3

      3. Leaf-margins never with slender, sharp, numerous teeth or cilia; oil-bodies homogeneous, small or minute, numerous (8-18 per cell); plants small and fragile, filiform and flexuous, to 1.5 cm long; leaves usually bilobed at least 1/4 - 1/3 (the lobes often divided into several-many supplementary lobes), or sometimes with 2-3 nearly equal lobes; plants 0.5-1.25 mm wide. ....Sectio BIDENTES (*P. tridenticulata, caduciloba*)

      3. Leaves (at least when mature) with several slender teeth or cilia; oil-bodies (in our species) segmented, formed of coarse, protuberant oil-globules, larger (to 7 x 10 μ), 3-6 per cell; plants larger, *ca.* 1.8-2.5 (3.2) mm wide x 1.5-3 cm long or more; leaves when mature rarely bifid for more than ¼ their length, the lobes (when present) almost constantly armed with supplementary teeth but not lobes. ....Sectio CHOACHINAE (*P. austini, P. sullivantii*)

2. Plants with asexual reproduction absent or by leafy propagula of the distal one-half (or more) of the leaf-lamina (which may become caducous eventually in *P. yokogurensis*); leaves never tending to be deeply or regularly bilobed when mature; plants pale or yellow to pure-green, the stems often brownish (but the leaves never more than olive-green); oil-bodies segmented; leaves rotund to ovate or ovate-falcate, rarely parallel-sided, widest basally or at middle, or parallel-sided. 4

4. Leaf-margins normally provided with 2-18 (25-32) coarse, ± irregular teeth or long cilia (these rarely reduced or vestigial); commonly reproducing by leafy propagula of the postical (more rarely also antical) leaf-surface (except Subplanae); leaf-shape normally ovate-triangular to narrowly ovate-falcate to rectangulate to lingulate, 1.35-3 × as long as wide; never reproducing sexually (in our species); branches at least in part terminal. (Perianths, where known, relatively short, often ± campanulate in profile, with mouth wide; width equal to or greater than length of postical keel; perianths usually included or short-exserted; leaves ± laterally patent when moist; archegonia usually less than 20 per gynoecium.) 5

5. Cells moderate in size, averaging 20-25 μ wide in the leaf-middle, usually quite collenchymatous, with several coarse-segmented oil-bodies; leaves not or weakly shiny, firm in texture; leaf-margins with teeth coarse, formed of little or hardly elongated cells, never ending in a uniseriate row of 4-6 cells that are 2-3.5 × as long as wide; asexual reproduction via leafy propagula present (but occasionally lacking under some environmental conditions). 6

6. Leaves essentially obliquely ovate to ovate-falcate to ovate-triangular, the postical base more or less strongly dilated (in consequence antical and postical margins ± distinctly convergent); leaves slightly to distinctly imbricate when moist, at least contiguous; leaf-margins with cells nearly isodiametric (below the marginal teeth), never averaging as much as twice as long as wide; leaves 1.3-1.9 (2.3) × as long as wide, postical leaf-base long or short-decurrent; if postical leaf-bases only slightly dilated and leaves nearly lingulate, the leaves spreading at an angle of 45-55°; gynoecia typically on leading or elongate axes. 7

7. Postical leaf-base short-decurrent, and little ampliate, the leaf-bases sufficiently distant so that the postical stem-surface is usually extensively exposed; postical leaf-bases not or very narrowly erect or reflexed, not showing crista-formation or water-sac formation; perianths (where known) with antical and postical keels ± equally long, shorter than the widely truncate mouth; the mature perianth included within bracts, campanulate to obdeltoid in lateral profile; underleaves normally minute, often ephemeral; leaves with postical margin at an angle of 50-80° with the stem usually, the leaves only moderately imbricate (exc. *P. floridana*); antheridia (always?) 1 per bract. 8

8. Leaves with distal portions largely caducous, irregularly so, leaving irregular, truncated stubs; brood-plantlets usually produced subsequent to dehiscence of apical propaguliferous halves of leaves; leaves excessively fragile,

rather transparent; plants to 3-6 × pseudodichotomously or fasciculately branched. ....Sectio YOKOGURENSES (*P. yokogurensis*)

8. Leaves persistent, producing blood-plantlets (propagula) that are caducous when mature; leaves not excessively fragile; plants usually diffusely monopodially or 1-2 × dichotomously branched. ....Sectio CONTIGUAE (*P. dubia, P. floridana, P. virginica, P. aspleniformis*)

7. Postical leaf-bases strongly ampliate, short or long-decurrent; leaf-bases closely juxtaposed, entirely hiding stem beneath, the decurrent base erect (crista-formation) to strongly reflexed (water-sac formation), the cristae or water-sacs forming two elevated lines on the underside of the stem; perianths (where known) with antical keel elongate, postical keel short, the oblique, broad, perianth-mouth shorter than antical keel; leaves with postical margin typically at 90-100° with stem, the leaves very densely imbricate, quite persistent; leaves with base and sometimes entire postical margin more or less undulate or crispate-undulate; underleaves conspicuous, often large. (Plants with perianths subtended by 1-2 elongating innovations, the perianths thus eventually pseudolateral, or in sinus between the long dichotomous innovations.) 9

9. Leaves postically short-decurrent (0.2-0.3 the merophyte length), the postical base of the leaf ampliate, but merely erect or only narrowly reflexed, forming a crista (but never a water-sac); leaves never undulate or crispate; underleaves usually lamellate (sometimes bifid), with dentate or ciliate margins. ....Sectio HYPNOIDES (*P. hypnoides*)

9. Leaves postically long-decurrent (0.5-0.8 the merophyte length), the postical bases either sharply reflexed, forming a crista, or tubularly convolute, forming a water-sac; postical margin of leaf sometimes strongly crispate or undulate; underleaves divided nearly to base into several laciniae or long, cilium-like divisions. ....Sectio CRISPATAE (*P. ludoviciana, P. miradorensis, P. undata*)

6. Leaves lingulate, essentially parallel-sided throughout, not dilated above postical base, when moist remaining remote (when dry characteristically tubularly convolute and becoming linear-spiniform); leaves averaging (2.0) 2.2-2.7 × as long as broad, the postical base very short-decurrent; underleaves minute; marginal cells forming a somewhat distinct border, the inner tangential walls strongly thickened, the marginal cells elongated, 2-3 × as long as broad usually; gynoecia terminal at the apices of a freely pseudodichotomous decompound shoot-system, on abbreviated terminal branches. ....Sectio PARALLELAE (*P. diffusa*)

5. Cells (at least in mature plants) large in size, of the *contigens*-type, thin-walled and with only small trigones, averaging (27) 28-35 μ wide in leaf-middle, with several very fine-segmented, opaque, granular-appearing oil-bodies; leaves shiny, delicate in texture, drying nearly flat, lying in a single, nearly flat plane

2. Plants with asexual reproduction absent or by leafy propagula of the distal one-half (or more) of the leaf-lamina (which may become caducous eventually in *P. yokogurensis*); leaves never tending to be deeply or regularly bilobed when mature; plants pale or yellow to pure-green, the stems often brownish (but the leaves never more than olive-green); oil-bodies segmented; leaves rotund to ovate or ovate-falcate, rarely parallel-sided, widest basally or at middle, or parallel-sided. 4

4. Leaf-margins normally provided with 2-18 (25-32) coarse, ± irregular teeth or long cilia (these rarely reduced or vestigial); commonly reproducing by leafy propagula of the postical (more rarely also antical) leaf-surface (except Subplanae); leaf-shape normally ovate-triangular to narrowly ovate-falcate to rectangulate to lingulate, 1.35-3 × as long as wide; never reproducing sexually (in our species); branches at least in part terminal. (Perianths, where known, relatively short, often ± campanulate in profile, with mouth wide; width equal to or greater than length of postical keel; perianths usually included or short-exserted; leaves ± laterally patent when moist; archegonia usually less than 20 per gynoecium.) 5

5. Cells moderate in size, averaging 20-25 μ wide in the leaf-middle, usually quite collenchymatous, with several coarse-segmented oil-bodies; leaves not or weakly shiny, firm in texture; leaf-margins with teeth coarse, formed of little or hardly elongated cells, never ending in a uniseriate row of 4-6 cells that are 2-3.5 × as long as wide; asexual reproduction via leafy propagula present (but occasionally lacking under some environmental conditions). 6

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7. Postical leaf-base short-decurrent, and little ampliate, the leaf-bases sufficiently distant so that the postical stem-surface is usually extensively exposed; postical leaf-bases not or very narrowly erect or reflexed, not showing crista-formation or water-sac formation; perianths (where known) with antical and postical keels ± equally long, shorter than the widely truncate mouth; the mature perianth included within bracts, campanulate to obdeltoid in lateral profile; underleaves normally minute, often ephemeral; leaves with postical margin at an angle of 50-80° with the stem usually, the leaves only moderately imbricate (exc. *P. floridana*); antheridia (always?) 1 per bract. 8

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9. Leaves postically short-decurrent (0.2-0.3 the merophyte length), the postical base of the leaf ampliate, but merely erect or only narrowly reflexed, forming a crista (but never a water-sac); leaves never undulate or crispate; underleaves usually lamellate (sometimes bifid), with dentate or ciliate margins. ....Sectio HYPNOIDES (*P. hypnoides*)

9. Leaves postically long-decurrent (0.5-0.8 the merophyte length), the postical bases either sharply reflexed, forming a crista, or tubularly convolute, forming a water-sac; postical margin of leaf sometimes strongly crispate or undulate; underleaves divided nearly to base into several laciniae or long, cilium-like divisions. ....Sectio CRISPATAE (*P. ludoviciana, P. miradorensis, P. undata*)

6. Leaves lingulate, essentially parallel-sided throughout, not dilated above postical base, when moist remaining remote (when dry characteristically tubularly convolute and becoming linear-spiniform); leaves averaging (2.0) 2.2-2.7 × as long as broad, the postical base very short-decurrent; underleaves minute; marginal cells forming a somewhat distinct border, the inner tangential walls strongly thickened, the marginal cells elongated, 2-3 × as long as broad usually; gynoecia terminal at the apices of a freely pseudodichotomous decompound shoot-system, on abbreviated terminal branches. ....Sectio PARALLELAE (*P. diffusa*)

5. Cells (at least in mature plants) large in size, of the *contigens*-type, thin-walled and with only small trigones, averaging (27) 28-35 μ wide in leaf-middle, with several very fine-segmented, opaque, granular-appearing oil-bodies; leaves shiny, delicate in texture, drying nearly flat, lying in a single, nearly flat plane

when moist; margins with teeth very sharp and strongly aciculate, some ending in uniseriate rows of 4-6 cells, each of which is 2-3.5 × as long as broad; often with 2-3 of the terminal teeth elaborated as incipient lobes; asexual reproduction absent; leaves remote to barely contiguous. ....Sectio SUBPLANAE (ACANTHOPHYLLAE) (*P. japonica ciliigera, P. echinata*)

4. Leaf-margins varying from entire to finely and ± regularly denticulate (with usually 20-35 [45] fine teeth); leaves broadly ovate to suborbicular to reniform (0.7) 1.0-1.4 × as long as wide, the strongly arched postical base dilated; asexual modes of reproduction absent, the plants regularly producing sex organs; branching normally entirely intercalary, from ventral end of leaf axil. (Perianths long-exserted, narrow, the finely dentate mouth less than one-half as wide as the length of the subequal antical and postical keels; leaves, on robust plants, somewhat postically secund or erect-appressed; cells of the *contigens*-type, with small to moderate trigones, *ca.* 30-35 μ wide or wider in leaf-middle; archegonia 20-25.) ....Sectio ASPLENIOIDES (*P. asplenioides, P. arctica, P. columbiana, P. satoi*)

Relationships of the above Sections.—Although, with our present fragmentary comprehension of the group, a "phylogenetic" tree for *Plagiochila* is impossible to derive, certain relationships appear evident. The writer believes that the groups lacking asexual propagative means (caducous leaves, propagula, etc.) are to be classed as more primitive. Among these are three sections, Zonatae (with *P. sharpii, semidecurrens*) and Asplenioides (*P. asplenioides, arctica*) and Subplanae or Acanthophyllae (with *P. echinata*). The first two sections have a similar leaf-form, a tendency towards very numerous, but short, marginal teeth of the leaves, a tendency towards adaxially appressed and often postically secund leaves, and a long perianth that is distinctly exserted, with the mouth much narrower than the perianth is long. They branch almost entirely by intercalary branches. However, the larger cells of the Asplenioides, their segmented oil-bodies, and the absence of a vitta suggest the two groups are only distantly related. Carl suggests the restriction of the name Heteromallae to this complex of sections.

A second complex of forms includes the types producing leafy propagula; this group includes the Contiguae (*P. floridana, virginica, aspleniformis,* etc.), the Yokogurenses (*P. yokogurensis*) the Crispatae (*P. undata, ludoviciana*), the Hypnoides (*P. hypnoides*) and the Parallelae (*P. diffusa*). These plants all agree in the generally relatively dull texture, the lack of distinct brown pigmentation, the cells of the *hypnoides*-type (less than 25 μ wide in leaf-middle, with discrete trigones that often bulge), frequent terminal branching, the green color of the leaves, and the perianth-form (with mouth wide, and at least postical keel ± short). The plants have a characteristic appearance, due to the generally few (5-15, occasionally 15-30) rather coarse teeth that are never aciculate, the usually densely chloro-

phyllose cells, the relatively narrowly ovate or ovate-falcate to ovate-lingulate leaves. Carl suggests the name Hypnoides for this group of sections. Among these sections, the Parallelae form the most isolated element, showing a distinctive, copious, deliquescent, dendritic branching. They appear to show some affinity to the Asiatic Frondescentes in this regard.

A third group of sections, essentially of tropical origin, is represented only by the Subplanae (*P. echinata, japonica* subsp. *ciliigera*) locally. These sections are characterized by delicate texture, green color, general absence of asexual reproduction, the often terminal and fasciculately aggregated androecia, and the *contigens*-like cells (*i.e.*, cells large, thin-walled, with small trigones, their width over 30 μ in the leaf-middle). A further tendency that appears to pull these sections together is the sharp tendency for laterally distichous leaves that are never very distant, usually flat (even in drying) and whose margins are usually strongly differentiated into narrow spines or cilia. The plants are not or only very diffusely branched (except that the sexual branches are commonly fasciculate). Carl suggests for this group the name Eury-Plagiochilae. The species of this group apparently produce both intercalary and terminal branches, as do the Hypnoides.

A smaller, less-developed element of the genus includes the delicate species, often with a shining cuticle and brownish cell-walls and always reproducing by caducous leaves (or leaf-lobes). The plants belonging to this complex show a well-defined tendency to have sharply bilobed leaves; the cells are moderately large (to 25 μ wide) and distinctly collenchymatous; no vitta is ever indicated; the leaves spread laterally or are slightly postically secund; branching is apparently wholly intercalary. To this complex I would refer the Bidentes and the Old-World Capillares, and also the Sectio Choachinae. The latter includes largely plants with segmented oil-bodies (while the Bidentes have them homogeneous), but the similarity in reproduction, and in many cases of leaf-form, the ability to produce caducous leaves and a brownish pigmentation (even when growing in diffuse light) all suggest a distinct relationship. In the writer's opinion, Carl is not correct in assigning the Choachinae to his "Heteromallae" — a group which should be restricted to types with persistent leaves. For the brownish plants with caducous leaves of great fragility, which encompass the present group, the writer would suggest the group name of Caducifoliae. This group agrees with the Heteromallae in that its species develop exclusively intercalary branches.

The postulated relationships may be summarized as follows:

Series HETEROMALLAE	Sectio ASPLENIOIDES (*P. asplenioides, satoi, arctica, columbiana*)
	Sectio ZONATAE (*P. sharpii, semidecurrens*)

Series HYPNOIDES	Sectio CONTIGUAE (*P. floridana, aspleniformis, virginica, dubia*)
	Sectio YOKOGURENSES (*P. yokogurensis*)
	Sectio HYPNOIDES (*P. hypnoides*)
	Sectio CRISPATAE (*P. ludoviciana, undata, miradorensis*)
	Sectio PARALLELAE (*P. diffusa*)
Series EURY-PLAGIOCHILAE	Sectio SUBPLANAE (*P. japonica ciliigera, rhizophora, echinata*)
Series CADUCIFOLIAE	Sectio CHOACHINAE (*P. austini, sullivantii*)
	Sectio BIDENTES (*P. tridenticulata, caduciloba*)

DISTRIBUTION PATTERNS OF OUR SPECIES OF PLAGIOCHILA

Because of the unnecessarily large number of existing binomials in the literature, and our extremely limited knowledge of most of these taxa, it is very difficult to attempt to treat the geographical relationships of our species. However, some start in elucidating the floristics of the species must be attempted, since several differing distributional patterns appear to characterize our species. These patterns clearly suggest that the effort by Carl to utilize a geographic approach in delimiting groups of sections has only a limited validity and usefulness.

1. Species of oceanic affinity, representing remnants of the old, Tertiary or pre-Tertiary flora, rich in members of the Magnoliaceae and Lauraceae. These species are limited strictly to "old" geographic regions which have not undergone glaciation, or submersion, since at least the start of the Mesozoic. Several species, to a greater or lesser extent, belong to this group, perhaps most typically *Plagiochila tridenticulata,* which has a range as follows: oceanic Europe, from SW. Norway to Ireland, coastal France, the Canaries and Azores, the Southern Appalachians from Virginia to North Carolina and Tennessee. Several other species-complexes exhibit, collectively, a similar range. For instance, *P. spinulosa* (of the oceanic portions of Europe), *P. sharpii* (Southern Appalachians; with a presumably conspecific race in Japan), and *P. semidecurrens* with its var. *grossidens* (coastal Alaska to Japan, and to the Himalayas), have a sum-total distribution which is classically oceanic. It is possible that the obligate asexual reproduction of *P. tridenticulata* has imposed an equally "obligate conservatism" on *P. tridenticulata,* as regards evolution into isolated, disjunct populations (only male plants are known from Europe; in the Appalachians apparently only female plants occur). Inversely, it is possible that correlated with the free production of sex organs (and presumably at least occasional sporophytes) in the *P. spinulosa-semidecurrens-sharpii* complex, we have had a somewhat higher level of regional differentiation (speciation and subspeciation), owing to

presumably greater opportunity for genetic recombination and meiosis, and consequently possibly differential selection in the several disjunct areas where the complex occurs.

Showing certain similarities in range to the above species, yet differing in significant details, are the regional members of the Subplanae-Acanthophyllae Complex, i.e. *P. echinata* and *P. japonica*. These two species are low altitude species, the first strictly confined to the Southern Appalachians, while a regional subspecies of the latter (subsp. *ciliigera*) is confined to the Ozarks. *P. echinata* is a vicariad of the east Asiatic *P. euryphyllon,* known only from Foochow, China; it may eventually be found to be a mere vicarious subspecies of the latter. *P. japonica* is widespread in Japan and elsewhere on the islands immediately south of Japan; the Ozarkian subsp. *ciliigera* may prove to represent an autonomous species, but is so close that I have preferred to treat it as a mere race.

Two other species represent a more restricted segment of the so-called Tertiary distribution pattern. These are *Plagiochila rhizophora,* known previously only from Japan but apparently also present on the Pacific Coast of North America, and *P. satoi,* which appears to be widespread in Japan, but also occurs on the North Pacific Coast of North America. These two species are apparently members of the North Pacific and Hyperoceanic series; they show a range rather similar to that of *Macrodiplophyllum.*

The nearly total sterility of most of the aforegoing species of *Plagiochila* is noteworthy. Equally significant is the fact that none of these species are able to reproduce asexually by reproduction of propagula. Asexual reproduction is either absent, or else by means of caducous leaves. It may not be coincidental that these species, except for *P. satoi,* all possess either homogeneous oil-bodies, which are of rare occurrence in the genus as a whole, or else possess very finely granular ones, which are perhaps even less frequent in occurrence within the genus.

It is possible that the *P. sullivantii-austini* complex, of the Southern Appalachians, also finds its closest affinity with this group of oceanic species. A distinct affinity of the former, at least, to *P. punctata* of oceanic Europe appears to occur.

The distribution of these oceanic species closely parallels the ranges of such oceanic species as *Pleurozia purpurea* (absent, however, in the Southern Appalachians), *Radula voluta* (western Europe; a single station in the Southern Appalachians, discovered by the writer in the Cullasaja Valley, North Carolina), *Cephaloziella* (*Cephaloziopsis*) *pearsoni* (western Europe from SW. Norway to England; discovered by the writer in several localities in the Southern Appalachians), and the *Acrobolbus wilsoni-ciliatus* complex (*A. titibuensis* of Japan, and *A. rhizophyllus* of the Southern Appalachians I regard as synonyms of the Himalayan *A. ciliatus; A. wilsoni* is definitely known only from westernmost Europe, in Scotland and Ireland). *Herberta hutchinsiae* (which I regard as a mere subspecies of the oceanic, Pacific *H. sakuraii,* of which the Appalachian *H. tenuis* is a mere race) has a similar range, involving westernmost Europe, Alaska, the Appalachians, and Japan (see Schuster, 1957c). It

should be emphasized that in many cases it is of little moment at present whether the segments of these complexes are regarded as portions of "Arten-kreise" or "Rassen-kreise," since no fundamental knowledge on the degree of biological isolation of these taxa is available. Braun (1955) has recently emphasized the subjective nature of the taxonomic treatment of such taxa.

2. Species showing a distinct connection between the Appalachian-Ozarkian Upland, and the upland of eastern Asia, and (probably) some affinity to the species of the tropical American mountains from Mexico southward. This group includes *P. japonica,* a widespread and polymorphous species of eastern Asia, which is represented in America by what can hardly be considered as more than a distinct subspecies in the Ozark Mountains. This species, in turn, exhibits unmistakable affinities to the species of the Sectio Subplanae (particularly to *P. hondurensis Herz.*) which are according to Carl limited to the Neotropics.

Allied phytogeographically, in several respects, to this group is *P. yokogurensis,* a species widespread at lower elevations in Japan. This is represented in the lower elevated areas (Piedmont and Coastal Plain) of the southeastern United States by a closely allied race, subsp. *fragilifolia.* No allied neotropical species have been recognized.

3. Species showing a distinct connection between the Southern Appalachian elements, and those of the uplands of Central America (and in particular, Mexico). *P. caduciloba* of the Southern Appalachians (from northern Georgia and South Carolina to Tennessee and North Carolina) is allied most closely to *P. cuneata,* particularly the var. *loriloba* Herz., occurring from tropical montane Central America into tropical montane, northern South America. The former species, limited largely to the cove forest (Mixed Mesophytic Forest), is another link between the old, Tertiary Forest of the Appalachians and that of the upland of Central America, in which the Magnoliaceae and Lauraceae play a prominent part.

The species of the preceding three groups exhibit some floristic features in common; they are all limited to upland regions which escaped glaciation and submersion within recent geological eras; they are largely limited to areas where remnants of the old Tertiary angiosperm floras persist; none of them reproduce via leafy propagula, but either lack asexual modes of reproduction, or reproduce via caducous leaves (or leaf-lobes). These groups stand in sharp contrast to the following three groups of species, whose history in our area appears, in most cases, to have been relatively recent.

4. Species of neotropical affinity, not wholly coastal in distribution in our area. This group includes several species (*P. ludoviciana, P. undata*) which recur at the inner edges of the Piedmont, or in the southern Appalachian gorges, and then are more common and widespread on the outer Coastal Plain. They appear to represent an element that was widespread during Pleistocene times in the Piedmont, when this area was presumably less hot and dry, with a more

"oceanic" climate; this element, presumably, has largely died out in the Piedmont (except for isolated stations of *P. undata*), migrating into the Coastal Plain during its Pleistocene emergence, and to a slight extent, perhaps, migrating into the southern portions of the escarpment gorges of the Appalachians. These species, then, appear to have survived the Pleistocene, and the immediate period before, at various elevated points in the Piedmont, and still occur there in various points at the juncture of the Piedmont and the mountains, as in the Estatoe Ravine, the Toccoa Falls and Tallulah Falls region of NE. Georgia, etc., as well as in the elevated Oligocene Island region of central Florida, which may have served as another source for the recent dispersal of these species. Consequently, their extant range represents a post-Pleistocene amplification of a probably rather wide pre-Pleistocene range in the same general region.

5. Species of neotropical affinity, coastal in distribution, but not representing recent invaders. In this group may be several species that occur in the Oligocene Island area of central Florida, but not in the recently emerged area of southern Florida, and to the north. *P. miradorensis, P. dubia* (the typical locally calcicolous phase), and *P. floridana* represent this category. These species are in several cases widespread in the Gulf Coastal Plain, and may occur as far north as the outer Coastal Plain of North Carolina; they are lacking (at least in typical manifestations) in the recently exposed areas lying to the south of the Oligocene Island region. To be classed here, as a presumed endemic, is *P. aspleniformis,* known to date only from the Oligocene Island region. Except for the latter and *P. floridana,* these species are widespread in Mexico and Central America, and in part appear to recur in the West Indies.

6. Species of neotropical affinity, in our area exclusively coastal in distribution, representing Pleistocene or recent invaders. Two species, *P. diffusa* and *P. hypnoides,* occurring mainly in the southern third of Florida, south of the Oligocene Island area, fall into this category. The first occurs from Bermuda and the Bahamas to Puerto Rico and Cuba, and presumably elsewhere in the West Indies; the second is a very widespread Antillean, Central American and South American tropical type.

It is of some interest that all these coastal species, of neotropical affinity (groups 4-6) represent species with free reproduction by propagula, representing the allied Sections Contiguae, Parallellae, Hypnoides and Crispatae. The final group, below, exhibits no affinities with any of the preceding groups.

7. Species of holarctic distribution, widespread in glaciated areas. Including the widespread, circumboreal *P. asplenioides,* of temperate to arctic regions, and *P. arctica* (presumably circumarctic in range). These are large-celled species, without asexual reproduction, lacking close affinity both floristically and phylogenetically to any of the foregoing.

SPECIES CONCEPTS USED IN THE PRESENT STUDY

As in other technical groups of organisms, the concept of species in *Plagiochila* is almost impossible to circumscribe on a basis that has other than a temporal, working utility. The absence of prerequisite experimental work for the definition of biological species means that a species concept has had to be arrived at from (a) morphological study, supplemented by (b) reasoning from the previously acquired knowledge of the modification-patterns in other leafy Hepaticae, and (c) a limited amount of study of the effect of environmental extremes on the form of a species.

In addition, several other axioms have been followed: (1) Two taxa, if occurring in the same region, but differing in slight but constant criteria, are probably good species; (2) two taxa, if with a strictly complementary range, and differing only slightly morphologically, are quite probably only discrete subspecies; (3) two taxa, even if very similar, but occurring growing under the same environment, or intermingled, are probably good biological species; (4) two taxa, no matter how distinct, if occurring in the same geographical range, but never found growing together, must be considered, *a priori,* with some suspicion.

The latter axiom has proved a very necessary one to maintain. So far as vegetative characters go, only three (oil-body type; mode of asexual reproduction; differences in cell size when large and obvious) appear to always represent unimpeachable "species characters." The rest of the vegetative plant (leaf form, dentition, leaf-orientation, trigone-development) appear to undergo such a vast amplitude of modification, and probably also much minor genetic variation, that study of a series of specimens, by the usual taxonomic techniques, leads to the eventual impression that specific lines are virtually impossible to maintain in some complexes. One is inevitably reminded of the statement of Douin (1916) on *Cephaloziella*: "dans le gametophyte, tout n'est que variations."

When one considers that only one (cell-size) of the three major criteria I rely on to separate species has been extensively used before in the classification of our species of *Plagiochila,* it becomes obvious that much future work on the genus is needed.

As in other groups of great difficulty, the student at first grossly underestimates the problems involved. After study of the type material, and a limited suite of specimens, the writer first arrived at the conclusion that the nearctic species of *Plagiochila* offered few intractable problems. A key could be prepared to separate adequately the nearctic species, using the type material. Study of several hundred collections, subsequently, soon showed that the species all represented polymorphic entities. Modification after modification had to be introduced into the descriptions, discussions and keys — and many key characters proved unreliable. Finally, the constellation concept became the only feasible one left for the circumscription of the more difficult species. This involved recognition that a species varies, not only genetically, but environmentally and temporally, to such a degree that it cannot be circumscribed, as a

rule, by two or three absolute criteria. Instead, an ensemble of criteria had to be utilized, *i.e.,* a constellation of features, all of which were likely to be individually unreliable taxonomically, but, taken *in toto,* made recognition of the species possible. For these reasons, it should be self-evident, that a completely satisfactory key to species cannot be made. For the same reasons, a lengthy discussion, under most species, of the features allowing separation from potentially similar species proved an absolute necessity.

It should be emphasized that much of the difficulty, regionally, with the Plagiochilae is the consequence of two factors that have not been adequately stressed previously: (1) The species often occur as localized and relict populations, the remnants of a wider Tertiary and possibly even pre-Tertiary distribution. Associated with this we find a high level of sterility and development of diverse modes of asexual propagation. The various taxa thus become static and rigid, in an evolutionary sense. Hence it can be expected that "new" species found regionally may well prove to be mere local manifestations or vicariads of species more widespread in other "old" areas. (2) With the reduction in range to local enclaves, where the species barely manage to survive, or with post-Pleistocene penetration into "new" areas, the species have in many cases been able to survive—or penetrate—as sterile, persistently juvenile or atypical manifestations, Since there is a great deal of reversion among the various Plagiochilae, when growing under difficult conditions, the correct interpretation of the various taxa is often a matter of the utmost difficulty. This is particularly the case with taxa now confined to a very few localities (such as *P. echinata* and *P. aspleniformis*), or with taxa which have spread northward from the tropics barely into the southeastern Coastal Plain (such as *P. dubia*). In understanding the limitations placed upon a morphological approach to the taxonomy of the group, such as is necessarily the case here, the preceding discussion on distribution patterns is pertinent.

THE BASIS FOR RECOGNITION OF PHYLADS AND TAXA

The criteria which the writer has found to possess specific (and in some cases sectional) value, and to be significant in indicating relationships, are systematically listed in the subjoined outline. The student should also refer to the more generalized treatment by Carl (1931a, pp. 24-36), in which the general variation and its significance are examined for the much more polymorphic *Plagiochila* flora of the world as a whole. For the limited number of regional species, the following treatment suffices.

Asexual reproductive criteria.—Since only *P. asplenioides,* among our species, is known to produce capsules, the various asexual modes of reproduction acquire a special significance in the classification of the species of *Plagiochila.* Although Carl (1931, 1932, 1933) has stressed these at some points, they have not been emphasized nearly enough in the broader classification of the genus. It is indeed unfortunate that in virtually all of the recent as well as older literature

the asexual reproductive mode is not noted. For instance, although all but a few among our species have decided asexual reproductive patterns, Frye and Clark note these in only two species. Similarly, Dugas (1928) in her quite arbitrary and schematic attempt at a classification of the genus does not attempt their use in the subdivision of the genus. The following outline, followed by a more detailed discussion of some of these reproductive modes, is of significance in the classification of our species.

a. Known to reproduce sex organs only, and with no mode of asexual reproduction ....*P. asplenioides, arctica, sharpii, semidecurrens, echinata, japonica*

aa. With some mode of asexual reproduction known, never (locally) found with capsules and usually known from one sex only. Several discrete modes of reproduction occur.

b. Leaves (or portions of them) regularly or occasionally caducous

c. Entire leaves caducous at base ....*P. tridenticulata, austini, sullivantii*

cc. Leaves with only portions caducous, the basal portions persistent

d. Reproducing by caducous leaf-lobes or elongate teeth; without formation of leafy propagula from the caducous portions ....*P. caduciloba*

dd. Reproduction by the caducous distal half of the leaves, which gives rise to leafy propagula ....*P. yokogurensis*

bb. Leaves persistent, but producing leafy propagula from the postical (more rarely also antical) leaf-surfaces, which become caducous at maturity ....*P. diffusa, virginica, undata, dubia, hypnoides, miradorensis, ludoviciana, floridana, aspleniformis,* etc.

In addition to the asexual reproductive modes outlined above, the neotropical *P. exesa* (see Carl, 1932, fig. 3) and *laceriflora* appear to reproduce by caducous teeth of the leaves (but, unlike in *P. caduciloba* the teeth are not highly morphologically modified for this purpose). The paleotropical *P. pluma* is reported as producing brood-bodies from the leaf-margins, evidently derived from leaf-teeth; see Carl (1932, fig. 2). I have not had opportunity to study the reproductive processes in these species. However, the few-celled brood-bodies of *P. pluma* are suggestive of the much more complex ones in *Xenochila.*

Degenkolbe (1938) draws a distinction between "Bruch—" and "Brutblätter"—i.e., between fragmenting leaves, and "brood" leaves, respectively. In the species with "Bruchblätter," or leaves with fragmentation via indeterminate lines, by completely irregular patterns, we find in addition to the dropping off of relatively unmodified teeth of the leaves (as in *P. exesa* and *laceriflora*), two other rather different types of reproduction by fragmentation occur, which may be dealt with in more detail since represented by local species:

Distal portions of leaves caducous.—In *P. yokogurensis* the distal one-half (more or less)of the leaf drops off, the line of breakage being irregular and quite indefinite. For that reason, the dichotom-Neotropics. In the Himalayan species, *P. diffracta* Herzog (1951)

ously divided shoot-system usually looks largely denuded (except for the persistent leaf-bases), exclusive of the tips of the branches where the leaves are as yet entire. Careful study of such relatively young leaves often reveals they may produce the earliest stages of leafy propagula (e.g., one to few-celled protruding cell-masses). Presumably, in this species, we have the quite unique situation of reproduction by caducous leaf-apices combined with propagula production. Perhaps related in this respect to *P. yokogurensis* is *P. furcifolia* Mitten, Trans. Linn. Soc. London, Ser. 2, 3(3) : 194, 1891 (described by and illustrated in Hattori, J. Jap. Bot. 26(6): 179-181, fig. 59, 1951). Hattori calls attention to the fact that in this species the apices of the leaves are mostly broken off, so that complete leaves are difficult to find. This species, and *P. yokogurensis* share not only the fragmenting leaves, but also the several-dichotomous aerial shoot-system, similar, rather large size, a basically similar, narrowly ovate leaf-form, similarly short-decurrent postical and long-decurrent antical leaf-bases; the cell-net is also of a similar type. *P. furcifolia* differs from our species, however, in the 1/5-1/3 bilobed leaves, and in the larger median leaf-cells (*ca* 24 x 30-35 μ).

Leaf-lobes freely caducous.—In *P. caduciloba* the numerous linear, peculiar leaf-lobes are freely caducous, breaking off in small, often few-celled, irregular plates, until nothing is left of the leaf, except for a broadly obcuneate, entire base. In extreme cases even the distal portions of the unlobed basal halves of the leaves are resolved into fragments. In no case is there any trace of initiation of propagula of the leaf-cells, at least while the leaf-lobes are still attached to the leaf. The pattern of fragmentation (Fig. 22: 3-5, 12-15) is described in more detail under the species concerned. A similar reproductive pattern occurs in *P. cuneata* (or at least its var. *loriloba* Herzog) from the we appear to have a similar, but even more extreme modification of this reproductive pattern. In this species, as in *P. caduciloba,* entire leaves are found only in the apical region, and start to fragment before attaining maturity. In *P. diffracta,* however, we find the additional specialization, apparently, of a persistent basal maturation of the leaves, resulting in elongation of the leaves for some time after the distal linear teeth, and after them, the distal portions of the lamina, have fragmented and disappeared. *P. diffracta,* in spite of its similar reproductive pattern, is at best distantly related to *P. caduciloba,* as is evident by the long-decurrent antical leaf-base, the few (6-8 usually) linear and largely uniseriate ciliiform marginal teeth, and in the much more robust size.

It is of some interest that at least one species of *Leptoscyphus* or *Leioscyphus* (*L. fragilis* Jack) shows reproduction by "Bruchblätter" —indicating a possible relationship between *Leptoscyphus* and *Plagiochila* that may prove closer than that which Evans (1898) has postulated to exist between *Mylia* and *Leptoscyphus.*

The second type of reproduction, by "Brutblätter," or caducous

leaves, treated by Degenkolbe, is represented among our species only in *P. austini, sullivantii* and *tridenticulata*. As Degenkolbe emphasizes "Die primitivste Art der Brutblattbildung ist bei einer Reihe von *Plagiochilen* . . . zu beobachten." This unspecialized type of reproduction by caducous leaves involves a free dropping off of nearly or quite unmodified vegetative leaves, of normal size. It occurs in species of two of Carl's sections (Choachinae and Bidentes). However, several species of *Plagiochila* (such as the extraterritorial *P. subalpina* and *naumannii*) show caducous leaves that differ morphologically from the persistent leaves. In these species, as well as in *P. acanthoda* of Central America (see Carl, 1932, fig. 1), the formation of caducous leaves appears to be limited to branches with small, atypical, bilobed leaves. Whether the caducous leaves are similar in size and form to the persistent leaves, or differ in size and form, the formation of the new plantlets appears to be largely similar. This usually takes place from a cell near the line of dehiscence of the leaf. Furthermore, a single caducous leaf usually develops only 1 or 2 of these regeneration-like plantlets.

Development of the leafy-propagula.—The presence, often in excessive abundance, of leafy propagula of the postical leaf-surface has been noted for a considerable time in *Plagiochila*. They were first noted by Spruce (1885), who spoke of the frequency of "Propagula, in the shape of leaf-suckers—minute branchlets springing from the surface of leaves, and each based on a single cellule. . . ." At times these are so abundant that it has lead such students as Schiffner (1901) to speak of the leaves as appearing "quasi Algarum caespitibus obsessa." Goebel (1930) and Carl (1933) have dealt with the ontogeny of these brood bodies. The following account, based on the nearctic species (in particular, *P. virginica* and *ludoviciana*) agrees in essence with these two previous studies, as it does with the discussion given by Degenkolbe (1938).

As has been pointed out, the development of the propagula is not limited to leaves of a particular age or development, with the exception that only mature or nearly mature leaves appear to develop them (difference from *Xenochila paradoxa!*). Furthermore, a single leaf, whether relatively young, or old, may show propagula of all ages, from the 1-celled state to the mature, caducous stages.

Carl (1933) emphasizes that propagula formation is almost always restricted to the underside of the leaves, even though he could find no anatomical differences between upper and lower leaf-surface. The similar restriction of various types of propagula to the lower leaf-surface in the Lejeuneaceae is also well-known, but not exclusively the case. Inversely, in the often epiphytic *Metzgeria crassipilis,* the brood-bodies appear restricted to the upper thallus surface. In the case of the Lejeuneaceae, Schiffner (1929) hypothesizes a physiological difference between upper and lower leaf-surfaces, and believes that "die dorsale Membran [of the leaf cells] früher ihre Dehnbarkeit

verliert." Carl, *loc. cit.*, states he has found only a single exception to the rule that the propagula occur restricted to the postical leaf surface; in *P. villosa*, he noted that the bracts as well as perianth bore propagula, and that the inner as well as external side of the perianth bore propagula. Study of the unfertilized perianths of *P. ludoviciana* and *P. miradorensis* reveals propagula often freely produced within the perianth. This has also, but more rarely, been observed in *P. floridana* and *P. dubia*, and probably occurs in many other species.

The true explanation for the general restriction of propagula to the postical leaf surface apparently lies in the fact that these delicate structures are more fully protected from desiccation when growing on the sheltered postical leaf-surfaces. Their occurrence on the inner perianth surface (corresponding to the upper leaf surface) is also indicative of the fact that brood body formation appears largely restricted to the less exposed surfaces of the gametophyte, a conclusion also arrived at by Carl.

This conclusion is reinforced by the repeated observation of propagula of the antical (adaxial) faces of the leaves in *P. dubia, P. floridana* and rarely in *P. ludoviciana.* In all three of these species, propagula are developed on the postical leaf surface almost indiscriminately in the distal half or more of the leaf. On the upper surface, the propagula are restricted to the posterior (ventral) margins of the leaf, and the peripheral portions of the lamina, *i.e.*, to those portions of the leaves which are somewhat sheltered owing to the overlapping of the antical portions of the leaves lying directly anterior to them. Evidently the restriction of the propagula is correlated very largely with those areas of the leaves that undergo desiccation last, and least frequently.

The development of the propagulum represents a process analogous to germination from the spore. The leaf-cell destined to give rise to a propagulum undergoes the following development: (1) the cell bulges outward and becomes strongly convex, its greater thickness usually being evident because of a greater opacity, compared with adjacent "normal" cells; (2) a wall parallel to the leaf-plane (tangential) divides this cell into a basal and a distal cell. The development of the propagulum proceeds from the distal cell in the following steps: (3) a radial wall (at right angles to the leaf surface) cuts the distal cell in half, followed by (4) a division by a radial wall at nearly a right angle to the first radial wall, of one of the two cells, resulting in a 3-celled body. From this point on, the development cannot be readily followed, because the individual cells protrude strongly, but there is the eventual development (5) of a more or less irregularly spherical mass of 8-12 or more cells. This does not proceed by an equal division of all cells, since the basal cells (attached to the original hold-fast cell) may cease division at an early stage in development.

From this rather irregular cell-body, whose later ontogeny appears to be relatively haphazard, we get the early development of (6) an apical cell with three cutting faces, which is responsible for the development of a linear body, undergoing an early division (7) into stem, and reduced lateral leaves, and usually minute underleaves.

At first the developing stem consists of three external cell rows, each row corresponding to one of the three rows of merophytes and developing uniseriate leaf and underleaf "Anlagen," but soon (8) the lateral merophytes undergo division, while the ventral merophytes remain one cell wide. Consequently, the earliest leaf-rudiments are only one cell wide, like the earliest underleaf rudiments, but the embryonic leaves, produced soon thereafter, develop from merophytes two cells and more wide (while the underleaf rudiments remain one cell wide and continue to originate from an undivided row of ventral merophyte cells). (9) The growing propagula soon develop minute lateral leaves, which, as soon as they attain a width of 2 cells or more, show the characteristic bifid condition of all juvenile Jungermanniacean leaves, while the underleaf traces remain undivided and filiform, 1-3, occasionally 4 cells long. Although most leaves show a bifid condition, the inherent plasticity of the embryonic leaves is evident by the fact that occasional or many leaves may be 3-dentate or trilobed. With the gradual elongation of the propagula (10) leaves of greater size are developed, which almost always retain the bifid form, thus show their juvenile condition, and there may be a restricted division of the ventral merophytes to the point where they become two cells wide and develop underleaves 2-3 cells wide. At, or before, this point in their ontogeny, the propagula are usually caducous.

Such brood-bodies, according to Carl, occur only in the Sectios Contiguae, Hypnoides, Crispatae, Parallelae, Villosae and Infirmae —sections which Carl admits are clearly related to each other (by their laterally spreading, approximate to imbricate, green leaves, the tendency towards clear development of underleaves, cells of the Hypnoides-type, in general, etc.).

Form and position of the female reproductive system.—The form of the perianth, and its position, appear to represent important criteria in the classification of the genus. Unfortunately, the absence of inflorescences in many species makes it difficult to utilize these characters fully. The position of the female inflorescences was first used as a major criterion by Spruce (1885). He divided the genus into two major groups, Cauliflorae (perianth terminal on main shoots or elongate branches, from beneath which there is almost invariably innovation on one or both sides) and Ramiflorae (perianth terminal on short ultimate branches of a freely dichotomously or pinnately branched system, the perianths not subtended by innovations).

Detailed study of our species has suggested that the division by Spruce is subject to intergradation. Although *P. asplenioides* often has perianths not subtended by innovations, as in the Ramiflorae, to which Schiffner (1893-95, p. 89) assigned it, the perianths occur on long, leafy shoots, and not on short ultimate branches (as in the Cauliflorae). In the little material seen of *P. semidecurrens,* a similar arrangement appears to occur, *i.e.,* the perianths often lack innovations but are on long, leafy shoots. This is regularly the case in

P. tridenticulata. By contrast, the propagula-developing series of sections (Contiguae, Hypnoides, Parallelae, Crispatae) all at least theoretically belong to the Ramiflorae. Well-developed plants are essentially pseudodichotomously branched, although weaker ones clearly monopodially so (with the branch much less robust), and the perianths are either terminal on leading axes, which may bear fertile innovations, or terminal on ultimate branches, and invariably subtended by 1-2 innovations. Little or no taxonomic stress can be laid on the number of innovations, at least in our species, since they vary from 1-2 within the same population. Unfortunately, in practice, variation in branching, sometimes even within the species, often serves to obscure the otherwise characteristic restriction of the gynoecia. For example, in *P. dubia* the gynoecia are occasionally terminal on elongate leafy shoots, which bear 2 innovations lying at right angles to each other that are soon again floriferous, and which in turn each bear a single innovation. The initial gynoecium, therefore, is "cauliflorous," the branch gynoecia clearly "ramiflorous." However, within the same population occur aerial shoots dividing 1-2-times pseudodichotomously, whose branches fork at the apex, with each short fork bearing a gynoecium, each of which may have 1-2 innovations beneath it. In the latter case we have a classical case of the "ramiflorous" condition, except for the occurrence of innovations.

The only species in which the "ramiflorous" condition is almost constantly well expressed is thus *P. diffusa.* However, even here an occasional gynoecium produces a subfloral innovation.

In general there is a gradual evolution from the primitive condition where the gynoecia are not restricted to short ultimate branches, associated with exclusively or nearly exclusively intercalary branching (Sectios Asplenioides, Zonatae) to the condition where the gynoecia are often on abbreviated lateral branches (Contiguae), associated with frequent terminal branching, to the ultimate condition found in the Parallelae (*P. diffusa*), where innovation-free gynoecia limited to abbreviated ultimate branches are linked with almost exclusively lateral, terminal branching. Unfortunately these steps, as we have seen, are not absolute; hence it is difficult to assign much systematic significance to them. For example, in *P. tridenticulata,* in which the gynoecia are on long, simple and leading aerial branches—and in which branching is exclusively intercalary—there are never subfloral innovations.

The presence (or absence) of gynoecial innovations, and the point of origin of these, is of some interest, although hardly of major systematic significance. Frequently related species, belonging to a single section, differ in this respect. For example our two species of the Sectio Bidentes are sharply contrasted: *P. tridenticulata* appears quite unable to produce subfloral innovations; *P. caduciloba* constantly producing innovations. Furthermore, in those species producing innovations there may be wide differences in (a) point of origin of the innovations; (b) whether the innovations remain sterile or again are

"floriferous." In this connection, see the discussion under *P. tridenticulata* and *P. sharpii.* The species of *Plagiochila* stand in sharp contrast to such groups as the Lejeuneaceae in that the point of origin of the innovation, or innovations, is subject to wide variation. For example, within the same species, some innovations may occur *below* the perichaetial bracts (the position in which they typically occur in Lejeuneaceae), but others are produced *above, i.e.,* in the axils of the perichaetial bracts, lying between bract and perianth. Both types of innovations may occur on a single plant, and, sometimes a gynoecium produces one type of innovation on one side, the other type on the opposing side. Not infrequently two or even three innovations arise from the axil of a single bract. There is also variation, within the species, as to the actual presence of innovations. In some species (*e.g., P. sharpii*) innovations are constantly produced; in others (*e.g., P. asplenioides*) they may be present or absent. There is, in the latter case, an apparent correlation between fertilization and sporophyte development, with suppression of innovations, and lack of fertilization and innovation initiation. How general such a correlation is, in the innovation-producing taxa, must be subject to further investigation.

The form of the perianth is unfortunately of limited taxonomic importance, except for the circumscription of species and small species-groups. The following types are familiar to the writer:

a. *Perianths elongate*, the postical and antical keels subequal, averaging 2-3-4 times as long as the vertically truncate mouth; the "tubular" type of Carl (1931, p. 35). Such regional species as *P. asplenioides* and *P. semidecurrens* possess this type of perianth, as well as such extraterritorial types as *P. gigantea.*

b. *Perianths strongly dilated*, except for the immediate "lips" of the bilabiate mouth, which are appressed, the perianth thus globose to pyriform; the dorsal and postical keels (when evident) subequal. None of our species appears to have perianths of this type, but the extraterritorial species *P. angulata* (see Carl, 1931, fig. 6b) has this type of perianth.

c. *Perianths short*, not projecting perceptibly beyond bracts, wide (widest at the vertically truncate mouth), campanulate to broadly obcuneate in form, laterally flattened or compressed. Among our species, *P. floridana* and *diffusa* have perianths of this type.

d. *Perianths with antical keel at least twice as long as the postical*, the very wide mouth thus strongly oblique (in lateral outline); the perianth superficially like type *a*, when seen dorsally, but in lateral view approaching type *c*, in that the mouth is very wide. Among our species, only the *P. ludoviciana-undata* complex appears to have perianths of this type.

e. *Perianth with a single antical*, but two postical, keels (the result, evidently, of the participation of the postical merophytes in the perianth formation). Known, to the writer, only in *P. tricarinata* Carl (1931, p. 74), from Costa Rica.

The presence or absence of a wing, or lamina, of the perianth-keels appears to be of limited taxonomic significance. For instance, in *P. ludoviciana* there may be no dorsal wing, or, occasionally a narrow, entire dorsal wing. In some species (*P. miradorensis*), the wing, or wings, may be armed. Constant differences between allied

species sometimes occur (*e.g., P. sharpii* has a wing, *P. "alaskana"* lacks it).

The form of the female bracts appears to offer few or no characters of taxonomic importance. In general, the bracts are equal to or somewhat larger than the vegetative leaves, have the marginal dentition or development of cilia more copious and marked (often indicated even when the vegetative leaves are subentire), but retain the basic form of the leaves. Spruce attempted to divide his Sectio Spinulosae (of the Cauliflorae) into two subgroups, based on whether the perianth was surrounded at base by a single pair of bracts (Exinvolucratae) or by several pairs of floral bracts (Involucratae). However, both Dugas (1929), and following her, Carl (1931), criticize this attempt as unnatural.

Stem and Branching.—Carl (*loc. cit.,* p. 24) has already emphasized that, within the genus, the stem anatomy is exceedingly uniform. The external 2-3, rarely 4-5 layers of cells are somewhat smaller in diameter, thick-walled, and often brownish-pigmented, contrasted to the larger-celled medulla, whose cells are thin-walled (but often with the angles somewhat thickened), with the walls colorless. Only in the extraterritorial *P. contingens* does a very sharp differentiation into cortex and medulla occur (*fide* Carl). The degree of development of the cortex is to a large degree influenced, at least in the more polymorphic species, by external conditions. In *P. asplenioides,* there are supposedly 3-5 thick-walled cortical layers; I find mostly a cortex 2-3 cell-layers thick, and exceptionally with a 1-2-stratose cortex so little differentiated as to simulate that of *Pedinophyllum.* The cortical and medullary cells, in all species studied, are furthermore elongate. The great elongation of the cortical cells (at least dorsally) serves as an important generic character, but appears sufficiently uniform as to make its use for species and group differentiation unreliable.

However, in the less specialized sections (Asplenioides, Zonatae) the cortical cells are much less elongated than in the members of the more specialized ones. In *P. asplenioides* and *P. arctica,* for example, the cortical cells average only 2-3 times as long as broad. By contrast, in the more advanced sections which bear various types of asexual reproduction, the cortical cells are much more elongated. In *P. diffusa,* of the Parallelae, for example, the cortical cells average 4-8 times as long as wide. In future work on the genus, this feature should be noted carefully, since it has at least a limited degree of significance.

Several of the extraterritorial species possess paraphyllia on the stem. In such species as *P. hirta, abietina,* and *hispida* these appear to occur along the entire axis, in the form of spinose protuberances, the stems appearing invested in a thick layer of spines. By contrast, in *P. trapezoidea, jensenii, intercedens, horridula,* the paraphyllia are in the form of lamellate or rib-like longitudinal protrusions, which may be entire or dentate on the margins. As is indicated by its name, *P. hamulispina* bears a third and anomalous type of outgrowth of the axis. None of the regional species bear any trace of such modification.

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Branching in *Plagiochila* and the allied genera *Chiastocaulon* and *Plagiochilion* is of three basic types: (1) postical, intercalary branching; (2) lateral intercalary branching, from the ventral halves of the leaf axils; (3) terminal, lateral branching, of the *Frullania*-type. Branching of the first type is characteristic of *Chiastocaulon* (which, however, also has lateral terminal branches) and *Plagiochilion* (in which some species appear to have only this type of branching, while others also possess lateral intercalary branching). In *Plagiochila, s. str.,* intercalary branching is exclusively or largely lateral, *i.e.,* of the second type, in the Sectio Asplenioides and Zonatae; it is also widespread in various other species of other sections. By contrast, terminal branches have not been observed in the Zonatae and Asplenioides (with the exception of *P. columbiana,* in which they are rare). In the Subplanae (*P. echinata*), there may be both postical and lateral intercalary branches, and a single postical intercalary branch has also been observed in *P. asplenioides.* Sections in which propagula develop (Yokogurenses, Parallelae, Contiguae, Hypnoides, Crispatae) regularly develop terminal branches, of the *Frullania*-type, in addition to lateral intercalary branches. The phylogenetic significance of the restriction of terminal branching to those sections needs to be investigated on a broader basis than I have done. Certainly, if the restriction is as sharp as it appears to be, the nature of the branching must be regarded as of very considerable taxonomic significance. Carl, and other students, have, however, hardly used it, and the mode of branching is barely mentioned in the large majority of diagnoses of the species.

In addition to the fundamentally different *types* of branches, there are readily apparent differences in *orientation* and *frequency* of branching as follows:

a. *Monopodial branching* (usually diffuse).—Characteristic of most of our species. The branches usually diverge at an acute but wide angle (most species), but may diverge at a nearly right-angle and may soon after their origin be geniculate, so that the branches come to lie subparallel to the main axis (*P. tridenticulata*). Branching of this type may be either terminal or intercalary.

b. *Pseudodichotomous branching.*—Characteristic, among our species, of *P. dubia, P. yokogurensis* and of the Crispatae, Contiguae and Hypnoides. We find here the branch becoming as vigorous as the main stem, which it somewhat displaces laterally, growing as rapidly as the main stem, and becoming as long, hence the main axis does not retain its dominant position. Such branching is exclusively terminal. The species of the Sectio Parallelae particularly frequently show such branching. Extraterritorial species, such as *P. dichotoma* and *P. gigantea,* showing such branching are illustrated in Schiffner (1893, p. 88). When optimally developed, a deliquescent, dendritic, decompound system results.

Unfortunately, there is no sharp distinction in many of our species between these two types of branching. In *P. dubia,* for example, the weak shoots have branching which is clearly monopodial, in that the lateral, intercalary branch is much less vigorous than the stem, which continues growth in the same axis. In contrast, strong shoots will be branched pseudodichotomously, with the

branch and main stem equally vigorous; such branching appears to be always terminal. Pseudodichotomous branching does not occur at all in the species which have only intercalary branching (such as those of the Asplenioides, Zonatae, Choachinae, and Bidentes). However, exceptions occur even here, as in *P. ovalifolia* and *P. lophophora* (see p. 112).

Specializations of these two types (1) the more primitive type with the main axis retaining its dominance and (2) the more derivative type, with the axis losing its dominance, the former analogous to excurrent branching, the latter to deliquescent branching, occur among extraterritorial species:

c. *Regularly pinnate branching.* — Characteristic of the Austral-antarctic Sections Durae and Abietinae. Derived from a monopodial mode of branching by the increase in frequency and regularity of branching, with branches regularly arising from the main axis only 2-3 merophytes apart.

d. *Fasciculate branching, with clustered ultimate branches.*—Absent in our species, but occurring in extraterritorial species (particularly from the Austral-antarctic).

The above branching-modes refer to the leafy, aerial shoot system. There is, of course, in addition, a greater or lesser degree of differentiation of a creeping, radicellose primary stem-system, from which the aerial leafy shoot system arises. In many cases, the differentiation between these two systems is absolute: the primary system possessing only leaf-rudiments of small size, but many rhizoids. This is the case in most of the species, and then often results in the typical growth pattern of the more diffusely branched species (such as *P. austini* and *caduciloba*), where we find the creeping primary stems give rise to simple or subsimple aerial stems at sufficiently infrequent intervals as to result in well-spaced aerial shoots. However, many of the less specialized species show but a slight degree of development of such differentiation into primary creeping leafless axes and secondary ascending leafy, aerial axes. An example of such a species is *P. virginica,* in which the primary radicellose creeping stems may be normally leafy, giving rise to ascending leafy shoots, usually free of rhizoids, except at the base. The ascending, secondary shoots, however, may revert to the primary type of shoot-system, since where they touch the substrate, they become radicellose and creeping, and after a period of creeping, may again give rise to aerial branches. This may, exceptionally, also occur in other species, such as *P. floridana* (Fig. 54:7), where the aerial shoots become attenuate, somewhat flagelliform and narrowed, with reduced leaves, and arch downward until in touch with the substrate, at which point they become radicellose and attached. Hattori also figures Japanese species with the same ability of the aerial shoots to become almost flagelliferous and stoloniferous in nature.

Occasionally, the more advanced types with a normal differentiation between stoniferous primary, and leafy, aerial, secondary shoot-systems revert to the simpler type of organization where the primary shoot-system is leafy, radicellose and creeping. This is particularly the case with the smaller, entire-leaved, more or less impoverished forms of *P. asplenioides* and *arctica,* which then may closely approach *Pedinophyllum* in facies.

Cell and Contents.—Among the most important, and to date most

neglected criteria for species and group characters are the nature of the cell, its wall, and particularly the size of the cell, degree of differentiation of marginal cells and of cells of the median portion of the base ("vitta"), and the nature of the oil-bodies.

a. *Cell-wall and size characteristics.*—Several distinct cell types are found among our species of the genus, which are best contrasted in the following outline form:

a. Apical cells small, usually 14-18 μ wide on an average; cells at base of leaf, along midline, forming a vitta of strongly elongated cells (3-6 $\times$ as long as wide); cells often producing large, salient trigones, even under conditions of very low saturation deficit. .... *P. sharpii, P. semidecurrens*

a. Apical cells larger; basal cells not differentiated as a vitta. .... b

b. Apical and median cells averaging less than 25 μ wide. c

c. Cell-walls able to produce brownish secondary pigment, even in diffuse light, the plants deep olive green to brown; plants with cells shiny when dry, usually strongly so; marginal cells never strongly differentiated. .... d

d. Cells able to produce large bulging trigones even under very moist conditions, but without intermediate thickenings. .... *P. caduciloba, P. tridenticulata*

d. Cells never producing greatly bulging trigones; xeromorphic forms usually with prominent intermediate thickenings, at least of longitudinal walls. .... *P. sullivantii, P. austini*

c. Cell-walls quite unable to lay down marked pigmentation, even in direct sunlight, the plants quite opaque usually, dull or nearly so; often with marginal cells strongly differentiated owing to the strongly thickened tangential walls; trigones large in xeromorphic forms, in extreme cases tending to be confluent longitudinally. .... *P. diffusa, virginica floridana, dubia, ludoviciana, undata, miradorensis,* etc.

b. Apical and median cells averaging 25-40 μ wide; cell-walls thin to slightly thickened (in marginal cells), with small to (in dry situations) weakly bulging trigones, never very prominently collenchymatous. ......*P. asplenioides, arctica, columbiana, japonica, echinata*

The five types cited above appear to belong to three chief types, among the six cell-types distinguished by Carl (1931 p. 28) namely the 1) *Contingens* type (cells with small trigones and a tendency for the walls to become somewhat thickened, at least in the several marginal cell-rows; cells large, over 30 μ on an average; no vitta; to this type belong *P. asplenioides, P. arctica* and *P. columbiana,* as well as *P. japonica* and *echinata.* 2) *Zonata* type (cells unusually small, the apical usually 14-18 μ, the basal forming a distinct vitta). To this type belong only *P. sharpii* and *semidecurrens.* Carl (*loc. cit.,* p. 29) would restrict this type to species of tropical Asia and the Austral-antarctic region. He further restricts it to species with relatively small trigones. However, our species have large trigones, as do many of the related Asiatic types. Perhaps the establishment of a different type for these vittate species is warranted. 3) *Hypnoides* type (cells intermediate in size between the *zonata*- and *contingens*-type, *i.e., ca.*

20-23 μ wide distally, *ca.* 20-24 x 30-35 μ basally; no vitta; trigones distinct to somewhat bulging). All our other species belong to this widespread type. However, one species shows an approach to the 4) *Bursata* type (cells like *hypnoides* type in size, but the longitudinal walls of the more or less elongate cells strongly and often nearly equally thick-walled; basal vitta absent). In *P. diffusa* we find an approach to this type of cell-net, in that the marginal 1-2 rows of cells belong to the *bursata* type, and are strongly elongate, while the interior cells are little elongate and belong more nearly to the *hypnoides* type.

The form of the cuticle is an excellent species character. For instance, the ancient *P. tridenticulata,* with smooth cuticle, can be separated at once from the neotropical *P. verruculosa,* which has a coarsely verruculose cuticle. Similarly, the European *P. spinulosa* (with verruculose cuticle), differs from the smooth-cuticled *P. sharpii* and *P. semidecurrens.* These differences, however, are between related species, thus of specific, and not of group, importance. In general, cuticular ornamentation is of rare occurrence in *Plagiochila.*

In various other groups of Hepaticae, the differentiation between marginal and interior leaf-cells is often of importance as a group-character (as in *Scapania* and *Diplophyllum*). However, Carl does not mention this feature in his discussion of *Plagiochila.* In the writer's opinion, certain species show a very definite tendency to produce margined leaves (most marked in *P. diffusa,* where it occurs in all modifications). In *P. sharpii* and its relative *P. semidecurrens* there is also a well-marked tendency for the development of a border of equally thick-walled cells, (Fig. 15:3, 6, 9) contrasted to the strongly collenchymatous interior cells. The rest of our species appear to be more variable in this characteristic: in some of these species there is a discrete tendency for the marginal cells to become equally thick-walled even when growing under conditions of relatively low transpiration-pressure (*P. asplenioides,* Fig. 9:1); others develop an obscure margin when growing under conditions of rather high saturation deficit (*P. floridana*); others never appear to show a tendency to develop a thick-walled border of marginal cells (*P. ludoviciana, undata,* etc.). It appears currently impossible to identify types sharply restricted to individual species or species-groups, on this basis—unlike in the genus *Scapania.*

b. *Oil-body characteristics:*

1. Oil-bodies small and homogeneous, mostly 8-16 per cell, glistening, at most very faintly 2-5 segmented with age. .... *P. caduciloba, tridenticulata, sharpii*
2. Oil-bodies small and less numerous (> 6-9 per cell) rather evidently coarsely segmented into 3-9 segments lying in 1 or partly in 2 rows. .... *P. diffusa, virginica, dubia.*
3. Oil-bodies formed of rather numerous (over 16 in surface-view) smaller oil-globules, thus more finely segmented; the globules, however, individually protruding, less than 1 μ each, appearing coarsely papillose,

the globules lying in 2-4, rarely 5 rows (in surface-view). ....*P. asplenioides, sullivantii, austini, undata, ludoviciana* (etc., the majority of our species).

The last two types intergrade freely with each other, and the distinction is therefore not a very useful one.

4. Oil bodies differing from all the preceding in being very finely segmented, thus appearing opaque and granulose, rather than with obvious, distinct segments. *P. echinata, P. japonica.* (The North Pacific *P. ovalifolia* and *satoi* also appear to possess such fine-segmented, granular appearing oil-bodies. In extreme cases, the spherules appear virtually confluent, but it is doubtful if truly homogeneous oil-bodies occur.)

As is evident from the above, the nature of the cells and oil-bodies serve to differentiate our species into several sharply distinct types, the *P. caduciloba-tridenticulata* complex (non-vittate species, with caducous leaves, homogeneous oil-bodies), the *P. sharpii-semidecurrens* complex (vittate species, with persistent leaves, ± homogeneous oil-bodies), and the rest of our species (non-vittate, persistent or caducous leaves, segmented oil-bodies). The first two groups appear to be sharply discrete, natural groups. The last, more inclusive group, in turn can be subdivided into three groups, the species of which show more affinity to each other than to those of other groups. The first of these groups include species with smaller cells, strongly collenchymatous in dry environments; the cells average less than 25 μ wide medially. To this group belong *P. dubia, virginica, undata, ludoviciana, miradorensis, diffusa, yokogurensis,* etc. The second group includes species with larger cells (25-40 μ wide), but with relatively distinctly segmented oil-bodies; this includes *P. asplenioides, arctica* and *columbiana.* The third and last of these groups include large-celled (25-36 μ wide) species, which have finely granular-appearing, opaque oil-bodies; this includes *P. echinata* and *japonica.*

Leaf.—Traditionally, leaf-form and insertion have been regarded as of primary importance in the discrimination of both species, and sections, in *Plagiochila.* The writer would place less emphasis on this organ, since its exceptional variability and plasticity, in numerous species, makes the use of the leaf difficult, if not impossible. However, within broad and sometimes vague limits, the form and orientation of the leaf and its type of insertion remain major criteria for species and group delimitation.

The leaf is basically derived from a bilobed ancestral type, as is the case with all Jungermanniales. In a considerable number of species (among them our *P. austini, P. tridenticulata*) the bilobed leaf-type is usually easily evident, even though often obscured by the development of marginal accessory teeth. In other species (*P. columbiana, P. asplenioides*) juvenile shoots often bear largely bilobed leaves, indicating an atavistic tendency to revert to the less specialized leaf-type. In still other species (*P. rhizophora, P. ludoviciana, P. yoko-*

gurensis, P. echinata) mature leaves may show two of the distal marginal teeth to be larger than the other more or less spinose teeth; these larger teeth undoubtedly represent the primary lobes of the leaf.

a. *Modification in lobing and dentition of the leaves.*—From the primary bilobed leaf-type (which may safely be regarded as the ancestral type), modification of the leaf takes place in three directions.

1. Development of few to numerous spinose, coarse teeth, with consequent virtual obliteration of the lobes. (*P. austini, P. echinata, P. ludoviciana,* etc.) In some species of this group, the cells of the teeth are little modified (*P. austini, P. ludoviciana, P. aspleniformis*), in others they become extremely elongate and slender (*P. echinata, P. japonica ciliigera*).

2. Development of even more numerous, small marginal teeth or denticulations, with no indication (on mature, normal leaves) of the ancestral bilobed leaf-form. (*P. arctica, asplenioides,* typical forms, *P. sharpii, P. semidecurrens.*)

3. Development of totally entire leaves (*P. arctica* and *asplenioides* forms, *P. dubia* var. *integrifolia, P. miradorensis* var. *convoluta,* etc., and numerous tropical species).

b. *Modification in leaf-shape.*—The ancestral leaf-form appears to have been ovate or subrectangular. From the ancestral condition may be derived three types; however, deviations from these basic leaf-forms are numerous, and are illustrated in Fig. 2, in Carl (1931, p. 26).

1. A narrowly rectangular leaf-form, with the basal portion no wider than the median (*P. austini, P. diffusa*). With inverse modification, the following leaf-forms result:

2. A broadly to narrowly ovate leaf-form, with the basal portion dilated (ampliate type) (*P. sharpii, ludoviciana,* etc.).

3. An essentially obovate leaf-type, with the base narrow (*P. sullivantii;* an extreme extension of this type is *P. caduciloba*).

From the broadly ovate leaf-type numerous modifications have been derived, including the reniform extremes (some phases of *P. asplenioides* and *P. arctica*) and the falcate extremes (*P. yokogurensis, P. miradorensis,* etc.).

c. *Modification in form of the leaf-base and antical margin.*—Modification of the leaf also involves modification in the degree of decurrence of the leaf-bases. In most species the dorsal base is more or less strongly decurrent (Fig. 25:7) reaching extremes (among our species) in *P. undata* and *ludoviciana* (Figs. 64:1, 71:1). In the majority of species, the postical base is hardly or much less decurrent (Figs. 8:4, 41:7) (*P. asplenioides, sharpii, diffusa,* etc.), but three species (*P. undata, miradorensis, ludoviciana*) show strongly decurrent postical bases (Figs. 62:1, 7, 10; 71:3, 6). Concommitant with the development of such strong decurrence of the postical base is usually a development of short merophytes (mod. *densifolia*), and the development of a strongly reflexed postical leaf-base (Figs. 67:16, 18; 69:3, 5, 11; 71:2, 3), and often a strongly reflexed antical leaf-margin (Figs. 61:1, 3a, 4). Such modifications are evidently correlated with the development of epiphytic habits, and represent evident adaptations for strongly intermittent moisture conditions—thus

are xeromorphic modifications. In well-developed cases, both the decurved and inflexed antical margin, and the pocket-like, convolute, postical base, must serve as "water-sacs", much as in the various Porellinae with which these species normally occur.

d. *Changes in form between leaves of the main stem and of the branches.*—In *Plagiochila* there are notoriously extreme variations between leaves of the main stem and of the branches (and often between those of primary and secondary branches), as well as between the lower and mature leaves of the main shoot. The lower leaves, both of main and lateral shoots, tend to be shorter and broader than normal leaves (Figs. 24:1; 45:4; 60:1) often show little or no dentition (but often revert to the primitive bidentate or bilobed type). With branching, the branch leaves are usually smaller than those of the main axis, and the branch leaves are often more spinose-margined.

It is important, in the study of the species, to make measurements (and study the dentition) of the mature leaves of main stems, and to use these for comparison (between one species and the next). However, occasionally two allied species can be separated much more easily on the basis of the respective form of the juvenile and branch leaves (compare Figs. 24:1 and 27:1).

e. *Position of the leaf, and orientation to stem.*—Three basic types of leaf-orientation are discernible in the genus. Unfortunately, there is apt to be very considerable modification with different levels of adaptation to progressively more xeromorphic conditions. These types may be distinguished as follows:

1. Leaves spreading laterally (thus lying nearly in a flat plane), the lamina of the leaf essentially flat. Two extremes may be distinguished, to which almost all our species belong:
   (a) Leaves at an angle of 40-50° with stem (*P. floridana*).
   (b) Leaves wide-spreading, at an angle of 65-90° with stem (*P. ludoviciana, undata, diffusa, virginica,* etc.).
2. Leaves postically strongly secund, even when moist. To this type belong xeric forms of *P. caduciloba* and *P. sharpii* (Fig. 18:1).
3. Leaves nearly erect, the adaxial face of the stiffly erect leaves nearly approximated to the lateral stem faces. *P. semidecurrens* belongs here, as well as forms of *P. asplenioides* and *arctica.*

The angle at which the leaves lie to the stem has been much emphasized. Carl (1931, p. 31) states "Ich sehe in der Blattstellung eines der allerersten Merkmale, das stetts innerhalb der einzelnen Sektion konstant bleibt." However, study of *P. asplenioides* and *P. sharpii* (see Figs. 19:4, 20:1-3) convinces the writer that this represents a very considerable overemphasis. In the least xeromorphic modifications (mod. *patulifolia-laxifolia*) the leaves spread horizontally, at an angle of 70° or more; but with more xeric conditions (mod. *erectifolia-densifolia*), the leaves become suberect, spreading at an angle of only 40-45°, in extreme instances even becoming erect-appressed!

It must be admitted that, although these differences in orientation are often useful as species and group characters, they are subject to much environmental modification. For example, in the *P. arctica-asplenioides* complex we find that prostrate plants from moist sites may have leaves spreading laterally (type 1), while vigorous, erect or

ascending plants (var. *devexa* of *P. asplenioides*) may have them rather strongly postically secund (Fig. 8:1); small, impoverished, xeromorphic, high arctic extremes (*P. arctica, P. asplenioides*) may have them virtually erect-appressed and slightly antically secund!

f. *Density of leaves.*—Depending on merophyte length, the leaves of the species of *Plagiochila* commonly range from remote to barely contiguous (*P. diffusa, P. sullivantii, P. austini*, etc., of our species), to contiguous to weakly imbricate (*P. dubia, virginica, floridana, aspleniformis*, and several other species). In all of these cases, the leaves are not sufficiently dense so that they are shingled, or overlap, at their postical bases; thus the stem remains exposed to view, when the plants are examined in their postical aspect. Less frequently the leaves are quite densely imbricate (*P. miradorensis, undata, ludoviciana, hypnoides*, in our species), owing to the somewhat shorter merophyte length, and in part, the greater dilation of the postical bases. In such cases, the leaves have the postical bases shingled or approximated to the point where, on mature shoots, the ventral face of the stem is completely hidden.

Since, in almost all species of the genus, the merophyte length of the mature shoot is subject to only a very slight degree of modification by different moisture conditions, the density of the leaves becomes a character of considerable significance, since it lends the species a readily recognizable, obvious facies. Only in the polymorphous and relatively unspecialized species of the Sectio Asplenioides is there considerable environmentally induced modification in merophyte length.

KEYS TO SPECIES AND SUBSPECIES

The identification of our species of *Plagiochila* is complicated by a) general absence of sex organs; b) frequent lack of any indication of asexual reproduction; c) the tendency for the worker to delay studying his material until after the death of the plants — *i.e.*, to a time when the cytological characters can no longer be used. Superimposed on this is the immense variability of many of the species. As a consequence, it has been deemed desirable to give three separate keys to species, in each of which the emphasis of the characters used is changed. The more troublesome varieties are keyed separately here; for the others see the text.

1. Plants dead (*i.e.*, without oil-bodies present). 2
    2. Key based largely on mode of asexual reproduction (or its absence), and on leaf form. ....Key I
    2. Key based largely on cell size and reproductive mode. ....Key II
1. Plants living, or at least with oil-bodies persistent: key based largely on type of oil-body and type of asexual reproduction. ....Key III

KEY I

BASED PRIMARILY ON LEAF FORM AND ASEXUAL REPRODUCTION

1. Leaves (or their distal portions) caducous, at least on some plants; cells medium sized. 2
    2. Leaves widest near or above middle, or rectangular: narrow near base, with postical margin not dilated basally; dorsal leaf-base hardly to shortly decurrent. 3

3. Leaves totally caducous, tearing free at base. 4
   4. Minute: to 1.5 mm wide; oil-bodies homogeneous; leaves bilobed, occasionally with 1-several accessory teeth. ....*P. tridenticulata*
   4. Larger: 1.5-3 mm wide; oil-bodies segmented; leaves (except when juvenile) with 5-9 or more sharp teeth. 5
      5. Leaves essentially rectangular: averaging over twice as long as wide; teeth of leaves never aciculate; leaves often showing a division of apex into two primary lobes. ....*P. austini*
      5. Leaves essentially obovate: averaging less than twice as long as wide; teeth of leaves narrow, usually spinulose or aciculate; leaves never with indication of bilobing. ....*P. sullivantii*
3. Leaves obdeltoid and deeply divided into linear lobes, which are caducous and fragment, leaving an irregular, truncate stub; oil-bodies homogeneous. ....*P. caduciloba*

2. Leaves ovate to markedly ovate-falcate, widest just above base: the postical portion above base obviously arched and dilated; distal halves of leaves irregularly caducous; leaves conspicuously and longly decurrent dorsally; plants olive-green to green throughout, shiny. ....*P. yokogurensis* subsp. *fragilifolia*

1. Leaves uniformly persistent; asexual reproduction by propagula (or absent). 6
   6. Base of leaf vittate; apical cells small: *ca.* 13.5-18 (20) μ wide or less; leaves broadly ovate to rotundate, with numerous spinous teeth; oil-bodies homogeneous or nearly so; usually strongly brownish; no propagula. 7
      7. Southern Appalachian; leaves with fine marginal teeth 2-4 (5) cells long; subapical cells (16.5) 17-20 μ wide; cells of vitta ± collenchymatous, 17-24 μ wide. ....*P. sharpii* subsp. *sharpii*
      7. Alaska to British Columbia; leaves with coarser marginal teeth, 3-6 (10) cells long in most cases; subapical cells usually (13.5) 14-16 (17) μ wide; cells of vitta ± equally thick-walled, 13-16 (17-18) μ wide. ....*P. semidecurrens* subsp. *grossidens*
   6. Leaf not vittate; apical cells 18-40 μ x 22-40 μ; oil-bodies segmented; leaves usually green (except *P. virginica caroliniana*). 8
      8. Median and subapical cells averaging (22) 25-40 μ wide or more, usually rather pellucid; asexual reproduction absent; usually exclusively with intercalary branching. (Leaves either with numerous fine, regular teeth, or entire, or if with a few strong teeth, these are usually spinose-ciliate to ciliiform [with the apical two often forming incipient lobes]; perianth, where known, with antical and postical keels subequal, without wings.) 9
         9. Leaves short-ovate to quadrate-ovate to suborbicular or reniform: usually (0.8) 1.0-1.4 × as long as wide; leaf-margins varying from entire to short-dentate, the teeth mostly very low and fine; plants nearly or quite dull. 10
            10. Median cells averaging (22) 25-33 μ wide; plants freely producing perianths, which are narrowly obcuneate in lateral profile and longly emergent, *ca.* 2.5 × as long as wide at mouth, the mouth always dentate. 11
               11. Leaf-cells medium-sized: the median 25-33 μ wide, averaging *ca.* 27-29 μ; submarginal and subapical cells *ca.* (19) 20-27 x 22-27 μ; basal cells along midline never tending to form an incipient vitta; leaf-margins with the dentition ranging from fine (teeth usually 1-3, rarely 4-5 cells high x

1-3 cells wide at base) to vestigial to absent; plants variable in size, but up to 5-7 cm long. Widespread. ....*P. asplenioides*[9]

11. Leaf-cells small: the median 21-27 μ wide, averaging 22-25 μ; submarginal and subapical cells *ca.* 18-21 x (18) 19-23 μ; mature leaves with basal cells along mid-line forming an incipient vitta of thick-walled cells; leaf-dentition normally much stronger, the teeth from 2-3 up to 5-7 cells high x (1) 2-4 cells wide at base, rarely weak or vestigial, never totally absent, on bracts and subfloral leaves even coarser and stronger; plants small, usually 1-2 (2.5-3) cm high. North Pacific. ....*P. satoi.*

10. Median cells large and pellucid, averaging 33-42 μ wide; perianths never produced (*P. columbiana*) or (*P. arctica*) short and broadly obcuneate and hardly emergent from between the connivent bracts, the mouth entire. (Confined to Piedmont of Southeast, or to Arctic.) 12

12. Leaves in large part provided with a few irregular teeth, at apex often broadly truncate or truncate-bilobed; occasional underleaves discrete, lamellate; dull; southeastern. ....*P. columbiana*

12. Leaves usually regularly rounded apically: entire-margined or with scattered fine regular teeth; underleaves always vestigial, of 2-several minute cilia; weakly shiny to dull; arctic. ....*P. arctica*

9. Leaves oblong-ovate to subrectangular: (1.2) 1.35- 2.3 × as long as wide, the margins with relatively few (4-12 [16]), long, spinous aciculate teeth, each terminating in a row of 4-6 ± strongly elongate cells (in weak forms the teeth sometimes less aciculate, then with a marked tendency for the apical 2-3 teeth to become elaborated as incipient lobes); plants strongly shiny, with leaves always laterally patent, usually nearly flat (even when dry). (Our populations never producing perianths; plants rare and of very restricted distribution in N.A., confined to non-glaciated areas.) 13

13. Leaf-apices not showing incipient bilobing: the aciculate marginal teeth never lobe-like; leaves narrow, oblong to rectangulate, (1.65) 1.8-2.3 × as long as wide, the leaf-apices rounded-truncate to rounded. Ozarkian. ....*P. japonica* subsp. *ciliigera*

13. Leaf-apices showing incipient bilobing: the 2 (rarely 3) apical teeth enlarged to form small lobes, occasionally to such an extent that the leaves are clearly bilobed for up to 0.25 their length; leaves oblong-ovate, relatively broad, 1.2-1.8 × as long as wide. 14

14. Plants with leaves rather broadly ovate, averaging 1.2-1.5 × as long as wide, with incipient apical lobes usually small; with usually 3-7 additional narrow, ciliiform teeth (of which 1-3 are often on the antical margin), in part formed of 5-6 superimposed elongated cells; light green to slightly brownish-tinged, never strongly brownish. Southern Appalachians. ....*P. echinata*

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[9] See also *P. major* (p. 143). The separation of the taxa of the Sectio Asplenioides is difficult. The synopses of species (pp. 116, 129) should also be consulted.

14. Plants with leaves narrowly oblong-ovate to ovate, averaging (1.3) 1.4-1.8 × as long as wide, with 2 (-3) of the apical teeth elaborated as strong lobes; with variously 0-2 or up to 10-12 smaller, *not* ciliiform spinose teeth, terminated at most by 2-4 superimposed, only moderated elongated cells; antical leaf-margin always edentate; deep green and ± brownish-tinged. Aleutian Isls. to British Columbia. ....*P. rhizophora* subsp. *confusa*

8. Median and subapical cells averaging 18-25 (rarely 28) μ wide; species regularly reproducing by propagula (except *P. undata*); leaf-margins with a limited number (usually 5-16) coarse teeth, these sometimes vestigial, the teeth never aciculate, more or less broad-based; leaves usually over 1.5 × as long as wide. 15

15. Leaves habitually densely imbricate, the strongly ampliate postical bases shingled, ± completely hiding the stem from postical view; dilated postical leaf-bases long or short decurrent, but always more or less erect, forming a crista, or convolute, forming a water-sac: underleaves usually discrete to large. 16

16. Leaves short-decurrent postically (decurrence 0.2-0.3 the merophyte length); entire postical leaf-margin sharply spinose dentate, including the basal region, which is somewhat cristate; underleaves essentially a ciliate-margined lamella (S. Florida only). ....*P. hypnoides*

16. Leaves long-decurrent postically (decurrence 0.5-0.8 the merophyte length); either basal, or distal, portions of leaves virtually or quite edentate (not restricted to S. Florida); underleaves deeply divided into laciniae or cilia. 17

17. Postical leaf-margin of sterile shoots not, or obscurely crispate-undulate, usually distinctly spinose-dentate (either near apex, or near base, or both); almost always with propagula. 18

18. Postical leaf-bases narrow, erect, forming a crista, of elongated, ± thick-walled narrow cells, edentate (or rarely with 1-2 teeth); leaf-apices usually sharply dentate; antical keel of perianth edentate; underleaves of 2-several laciniae or lanceolate lobes. ....*P. ludoviciana*

18. Postical leaf-bases dilated, reflexed and convolute, forming a tubular water-sac, of collenchymatous, scarcely elongated cells, usually bearing 2-6 spinose teeth; leaf-apices entire to weakly dentate; antical keel of perianth 2-4-dentate; underleaves of 2-several linear, uniseriate cilia. ....*P. miradorensis*

17. Postical leaf-margin of sterile shoots strongly crispate-undulate; leaf-margins entire or virtually so (except for 1-several low teeth near apex); propagula usually absent. ....*P. undata*

15. Leaves always approximate to laxly imbricate, rectangular to rather weakly ovate, the postical leaf-bases not to moderately ampliate, not shingled (closely imbricate only in *P. virginica euryphylla,* which see), leaving the stem largely exposed in postical view; postical leaf-bases short-decurrent, the decurrent strip flat or narrowly erect, at most; underleaves obsolete or virtually absent. 19

19. Leaves short-rectangular to quadrate-rectangular, broadly subtruncate at apex, 1.1-1.25 (1.4) as long as wide, with small,

irregular teeth confined to near apex; cells leptodermous to equally thick-walled (more so on margins), with minute trigones; subtropical. ....*P. aspleniformis*

19. Leaves either ovate (and widest just above base) or narrowly rectangular, usually at least 1.3 × as long as wide; cells collenchymatous (except mesic extremes), with median cells always with walls thin (unless the bulging trigones confluent). 20
    20. Leaves contiguous to imbricate, more or less ovate: the postical base slightly to strongly dilated and arched (however, in *P. floridana* barely dilated and nearly straight; this species differs from *P. diffusa* in the rather distinctly imbricate leaves): the greatest leaf-width (of the flattened leaf) thus subbasal; leaves not strongly margined: the marginal cells not set off as a border, rarely extremely elongate. 21
        21. Mature shoots with leaves spreading at 65-75° from stem-apex, typically (1.0) 1.3-1.8 × as long as wide when flattened); habitually sterile; not Coastal Plain: West Virginia to South Carolina and northern Georgia 22
            22. Leaves broadly ovate, strongly ampliate above the postical base (length: maximal width = *ca.* 1.0-1.35:1); the rounded, ampliate postical leaf-base, when flattened against stem, reaching across, and usually slightly beyond stem; stems thick, fleshy; leaves shrinking and postically secund in drying, slightly postically deflexed and convex when moist; leaves closely imbricate, long decurrent antically, entire and ovate-pointed, weakly bidentate, or distally sparingly and obscurely dentate. ....*P. virginica* var. *euryphylla*
            22. Leaves narrowly ovate to rather weakly ovate, little ampliate above postical base (length: maximal width = *ca.* 1.45-2:1); postical base of flattened leaf not reaching across stem; stems slender, rather wiry; leaves, in drying, not postically secund, when moist not at all postically secund, nearly flat; leaves distant to very weakly imbricate or contiguous, slightly decurrent antically, usually sharply spinose-dentate. 23
                23. Trigones varying from absent to small and barely bulging; pure green, typically robust, ± highly ramified plants. ....*P. virginica* var. *virginica*
                23. Trigones (even in pure green modifications) coarse and bulging, nearly or quite confluent, in xeric (brown) forms strongly confluent; small plants with simple or subsimple aerial stems. ....*P. virginica* var. *caroliniana*
        21. Shoots, at least on distal portions, with leaves suberect, spreading at an angle of 40-45° (on older portions sometimes at an angle of 65-75°); leaves typically 1.9-2.4 × as long as wide, when flattened, the postical base barely or weakly dilated: the leaves thus almost subrectangular or narrowly ovate; leaves sometimes with teeth reduced or vestigial; frequently with sex

organs; propagula usually in part on adaxial leaf faces. Coastal Plain: SE. North Carolina to Florida, to S. Mississippi and Louisiana. 24

24. Mature, robust stems with widely spreading leaves (65-75°), whose postical bases are somewhat ampliate and whose postical margins lie nearly (but usually not quite) at right angles to stem; leaves with teeth varying from small to weakly spinose; perianth mouth with usually relatively low, inconspicuous teeth. ....*P. dubia*

24. Mature, robust stems with leaves all erect-spreading (40-50°), whose postical bases are not or hardly ampliate and whose postical margins are clearly erect-spreading; leaves always sharply, often spinose-dentate; perianth-mouth with crowded cilia or narrow laciniae. ....*P. floridana*

20. Leaves remote, rectangulate, 2.0-2.5 (3.0) × as long as wide, parallel-sided, the postical base neither dilated nor arched; leaves strongly margined with 1-2 rows of elongate cells, whose tangential walls are strongly thick-walled to form a border; leaves distant, spreading at 65-75°, in drying tubular-convolute; teeth of leaves few and low, largely confined to near the truncate-rounded apex. S. Florida. ....*P. diffusa* (= *P. smallii*)

KEY II

BASED PRIMARILY ON CELL SIZE AND REPRODUCTIVE MODES

1. Cells large: on mature plants the median averaging (22-25) 26-38 (42) μ wide; oil-bodies papillose or segmented; leaves persistent and without propagula, without any mode of asexual reproduction. Branching normally exclusively intercalary; leaves not vittate at base. 2

2. Leaves bearing a few (3-9, rarely 12-18) spinose teeth, each terminated in a uniseriate row of 2-6 strongly elongate cells (and/or leaves showing incipient bilobing); marginal cells often ± tangentially elongated; oil-bodies ± finely granular-segmented; leaves ovate or oblong-ovate to ± rectangulate; plants strongly shiny, with flat, laterally patent leaves that are never postically secund. (Sectio SUBPLANAE.) 3

3. Plants Appalachian or Ozarkian in range, relatively large (2.8-3.5 mm wide usually), pellucid green to lightly yellow-brown; leaves with usually (5) 6-13 slender, ciliiform teeth, the longer ending in a row of 5-6 elongated superimposed cells; leaf-apex with incipient bilobing absent or slightly marked, the leaves never simply 2-3-lobed. 4

4. Leaves broad, ovate-oblong, averaging 1.2-1.6 × as long as wide, the leaf-apices usually conspicuously bilobed, the lobes running out in cilia (in addition to the marginal cilia); male sex only known; Appalachian. ....*P. echinata*

4. Leaves narrow, oblong to narrowly rectangulate, (1.65) 1.8-2.3 × as long as wide usually, the leaf-apices usually subtruncate, not or inconspicuously bilobed; habitually sterile; Ozarkian. ....*P. japonica* subsp. *ciliigera*

3. Plants North Pacific in range, small (1.8-2.4 mm wide usually), ± strongly brownish-tinged; leaves with 2-5 or up to 15-18 marginal teeth, none of which are ciliiform, the apical 2-3 usually elaborated

as obvious terminal lobes; leaves ovate to oblong-ovate, 1.3-1.8 × as long as wide. ....*P. rhizophora* subsp. *confusa*

2. Leaves entire or armed with small, merely acute teeth (whose apices are formed by at most 2-3 (4) superimposed, usually nearly isodiametric cells); marginal cells nearly isodiametric; oil-bodies coarsely segmented; leaves ovate or quadrate-ovate to rotundate-reniform, averaging (0.8) 1.0-1.4 × as long as wide; plants nearly or quite dull, with ± deflexed leaves (or with them suberect or erect-appressed). (Sectio ASPLENIOIDES) ....see Couplets 10-12 in preceding key (p. 98)

1. Cells smaller in size, either 14-18 μ wide or 18-25 (26) μ wide in the leaf-middle; with some mode of asexual reproduction (or oil-bodies homogeneous). 5

5. Subapical cells averaging (13.5) 14-19 (20) μ wide; median basal cells very strongly elongate, 3-6 × as long as wide, forming a short vitta; cells with homogeneous or finely granular oil-bodies; without any mode of asexual reproduction; leaves rotund-ovate to ovate, ampliate, usually (0.8) 1.1-1.5 × as long as wide, bearing usually 12-30 regular, sharp, relatively fine teeth; leaves strongly deflexed and postically secund, shiny; usually brownish. (Sectio ZONATAE) 6

6. Apical and subapical cells 13.5-16 (17) μ wide; antical leaf-margins arched; marginal teeth of leaves relatively coarse; leaves rather broadly rounded distally; plants known only from female sex; cells of vitta equally thick-walled, 13-17 (18) μ wide. ....*P. semidecurrens* subsp. *grossidens*

6. Apical and subapical cells (16.5) 17-19 (20) μ wide; antical leaf-margins straight; marginal teeth of leaves rather fine and regular; leaves ovate, rather narrowly rounded distally; known from male and female sex; cells of vitta collenchymatous, (17) 19-24 μ wide ....*P. sharpii* subsp. *sharpii*

5. Subapical cells 18-25 (26) μ wide; basal cells 1-2 × as long as wide, not forming a vitta; oil-bodies segmented (or leaves fragmenting or freely caducous); leaves ovate to rectangulate to obovate or obdeltoid, variously dentate; leaves not sharply postically secund; with some mode of asexual reproduction. 7

7. Asexual reproduction by means of basally caducous leaves (or caducous, linear, leaf-lobes); plants at maturity usually brownish, shiny, small (0.5- 2.25 [2.5] mm wide); leaves rectangular to obovate or obdeltoid, narrow-based; leaves not to very short-decurrent postically, ± distant to contiguous. Exclusively Appalachian in distribution. 8

8. Leaves tending to be wholly caducous, deciduous at the base, varying from rectangulate to obovate, bilobed to dentate to spinose-dentate or ciliate-dentate, the teeth persistent. 9

9. Plants small: 1.25-2.35 (2.5) mm wide; leaves tardily caducous usually, the mature ones dentate to ciliate-dentate (but sometimes also with an indication of lobes); oil-bodies segmented (Sectio CHOACHINAE). 10

10. Leaves rectangulate, ± twice as long as wide, often with a decided indication of 2 sharp apical lobes (with the dentition superimposed); teeth of leaves broad-based, short. ......*P. austini*

10. Leaves ± obovate, usually much less than twice as long as wide, never bilobed; teeth of leaves ± spinose or ciliiform, narrow-based. ....*P. sullivantii*

9. Plants minute: 0.5-0.8 (1.0) mm wide; leaves readily and freely deciduous, the stems often largely denuded; mature leaves 2-lobed, often with 1-several accessory teeth; oil-bodies minute, homogeneous. (Sectio BIDENTES, p.p.) .... *P. tridenticulata*

8. Leaves essentially obdeltoid, deeply divided into numerous linear lobes, the lobes fragmenting and deciduous (leaving irregular, obdeltoid stubs attached permanently to the stem); oil-bodies homogeneous. (Sectio BIDENTES, p.p.) .... *P. caduciloba*

7. Asexual reproduction (very rarely absent!) by means of propagula, produced in great numbers from the surface (usually postical) of mature leaves (in *P. yokogurensis fragilifolia* the tardily propagula-bearing distal portions of the leaves are irregularly caducous, at least with age); plants usually dull or weakly shiny, their leaves green to yellowish-green or olive-green; plants robust, 2.2-5.5 mm wide at maturity; leaves usually ± ampliate, the postical base slightly to distinctly expanded, the leaves thus ± ovate (except *P. diffusa* and *aspleniformis,* in which the leaves are rectangular); leaves ± long-decurrent antically; oil-bodies always segmented. 11

11. Leaves contiguous to densely imbricate, ovate to ovate rectangulate, at least slightly dilated postically (*the postical margin distinctly arched*), in drying variously convolute, but not becoming tubular, approximate to closely imbricate, 1.2-1.9 (rarely 2.1-2.4) × as long as wide; plants sparingly, often monopodially branched. 12

12. Leaves approximate to weakly imbricate, *short-decurrent postically,* ± *weakly ampliate,* varying from ovate-rectangular to ovate falcate to oblong; mature plants, in postical view, with stem normally extensively exposed, the postical leaf-bases not closely shingled; underleaves absent or vestigial; postical leaf-bases flat to very narrowly reflexed, *never with formation of a distinct crista or water-sac.* (Sectios CONTIGUAE, YOKOGURENSES) 13

13. Leaves widely spreading (65-85°), the anterior (postical) margins commonly nearly or quite at right angles to stem; propagula only on abaxial faces of leaves; habitually sterile. 14

14. Leaves distinctly ovate to ovate-triangular, or ovate-falcate, ampliate above postical base, varying usually from 1.3-1.7 (2.0) × as long as broad, ± sharply spinose-dentate; cells varying from thin-walled with minute or no trigones, to strongly collenchymatous; never equally thick-walled. 15

15. Leaves ovate to ovate-triangular, usually 1.3-1.55 × as long as wide, persistent, not fragmenting; plants dull; underleaves virtually absent; antical leaf-margin straight or weakly arched; leaves ± short-decurrent antically, the line of insertion 0.75-0.95 the maximal leaf-width; Appalachian. 16

16. Leaves broadly ovate, strongly ampliate at postical base (length 1.0-1.35 × the maximal width), closely imbricate, the stem in postical aspect nearly or quite hidden. ....
.... *P. virginica* var. *euryphylla*

16. Leaves narrowly to rather weakly ovate to ovate-falcate, little ampliate at postical base (length usually 1.45-2.0 × the maximal width), weakly imbricate or contiguous, the stem in postical aspect freely exposed. 17

17. Subapical and median cells 20-25 (26) μ wide, with minute to barely bulging trigones; plants green, typically with aerial shoots ± ramified. .... *P. virginica* var. *virginica*

17. Subapical and median cells 16-20 (21) μ wide, with bulging to confluent, coarse trigones; plants ± brownish, with short, simple aerial stems. .... *P. virginica* var. *caroliniana*

15. Leaves narrowly ovate-triangular to ovate-falcate, usually 1.55-1.75 × as long as wide, the distal portions usually freely caducous with age, leaving truncated stubs; plants ± shiny; often with distinct, if small, underleaves; antical leaf-margin distinctly concave; leaves long-decurrent antically: the line of insertion 0.95-1.2 the maximal leaf-width; trigones absent or minute; Piedmont and Coastal Plain. .... *P. yokogurensis* subsp. *fragilifolia*

14. Leaves oblong to oblong-ovate or rectangulate, to 1.2-1.4 × as long as wide, ***not ampliate above base,*** broadly rounded-truncate at apex, weakly dentate; plants shiny (at least when young), clear yellowish-green usually; cells equally thick-walled (the marginal ones, and several rows at antical and postical bases usually very strongly so!), without obvious, large trigones. Coastal Plain. .... *P. aspleniformis*

13. Leaves (except rarely a few at bases of old stems) erect-spreading to suberect (40-45, occasionally 50-55° with stem), below sometimes obliquely (55-65°) spreading, the anterior margins commonly at an acute angle with stem; leaves with postical base not or little ampliate, narrowly ovate-rectangular, *ca.* 2.0-2.4 × as long as wide; androecia and perianths commonly produced; propagula often in part on adaxial faces of leaves. Coastal Plain. 18

18. Leaves somewhat ovate, dilated at postical base, fine-dentate to subentire; older leaves commonly more widely spreading (65-75°); perianth mouth with rather close or distant, fine to moderate teeth. .... *P. dubia*

18. Leaves virtually narrowly rectangulate, not or barely dilated at base, coarsely spinose-dentate, usually truncate at apex; older leaves usually nearly equally erect (45-55, rarely 60-65° with stem); perianth mouth strongly spinose-ciliate. .... *P. floridana*

12. Leaves closely imbricate, strongly ampliate, obliquely ovate to ovate-falcate to ovate-triangular; mature plants with postical stem surface quite obscured by the ampliate, shingled postical leaf-bases (and decurrent strips); postical leaf-bases strongly reflexed (with formation of a water-sac) or ± sharply erect (crista-formation); underleaves discrete, often large; confined

to Coastal Plain and Piedmont from North Carolina southward. 19

19. Leaves postically long-decurrent, the decurrent strip extending down for more than half the merophyte length, *on mature leaves;* postical leaf-bases edentate (or else reflexed to form a water-sac); underleaves divided virtually to base into 2-several ciliary or lanceolate divisions. Sectio CRISPATAE. 20

20. Leaves with entire postical margin strongly crispate-undulate, entire or with 1-several minute teeth; leaf-apices entire or with 1-several obscure, low teeth; propagula usually lacking. ....*P. undata*

20. Leaves with postical margins not, or shallowly, undulate, usually with several sharp, conspicuous teeth (and also with conspicuous teeth near apex), or else with a reflexed basal pocket bearing 1-several sharp teeth; propagula always present (except in extreme shade forms). 21

21. Postical leaf-bases erect, forming a crista, entire (rarely with a single tooth), the dentition gradually becoming evident in distal two-thirds of leaf; cristate base of narrow, elongate cells, with usually ± equally thickened walls; underleaves of 2-several lanceolate-laciniate divisions, several cells wide at base. ....*P. ludoviciana*

21. Postical leaf-bases reflexed to form a water-sac, bearing (with isolated exceptions) 2-5 sharp teeth or cilia, the distal portions of leaves varying from entire to sparingly dentate with low and scarcely sharp teeth; decurrent postical base of little elongated, prominently collenchymatous cells; underleaves of 2-several elongate cilia, 1-2 cells wide at base. ....*P. miradorensis*

19. Leaves postically short-decurrent, the short-decurrent strip somewhat circinate, elevated to form a weak crista, never reflexed-convolute; postical leaf-bases with 1-several sharp teeth, the dentition extending from base to the ± truncate-rounded apex, regular, sharp; underleaves typically of a distinct lamella, fringed or armed with teeth or cilia. Sectio HYPNOIDES ....*P. hypnoides*

11. Leaves distant, narrowly rectangulate, the posterior margin nearly or quite straight, parallel to the straight antical margin, in drying tubular-convolute and becoming very distant, usually 2.0-2.5 × as long as wide; teeth rather fine, largely confined to apical and subapical region; leaf-margins distinctly bordered by a row of marginal cells, separated by a thick wall from the interior cells; plants copiously, pseudodichotomously branched. Only in a few hammock-forests in the southern tip of Florida. ....*P. diffusa*

KEY III

BASED PRIMARILY ON OIL-BODIES, REPRODUCTIVE MODE, AND CELL SIZE

1. Oil-bodies homogeneous or appearing so (rarely with age faintly granular or weakly transversely barred); only with intercalary branching; plants of

the Southern Appalachians or Pacific Coast, tending to be brownish-tinged; perianths ± narrowly obdeltoid to obcuneate, the keels as long or longer than width of mouth. 2

2. Leaves broadly ovate to subrotundate, long-decurrent antically, persistent, bearing many (usually 12-25) sharp, marginal teeth; leaves vittate at base; normally with 1-2 subfloral innovations. Sectio ZONATAE. 3

3. Apical and subapical cells 13.5-16 (17-18) μ, thick-walled, if with large trigones these ± confluent; cells of vitta ± equally thick-walled, 13-16 (17-18) μ wide, averaging up to 4-6 × as long as wide; oil-bodies large, 2-4 (5-6) per cell; marginal teeth of leaves rather coarse; perianth narrowly obcuneate, truncate at mouth, the keels not winged; North Pacific. .... *P. semidecurrens* subsp. *grossidens*

3. Apical and subapical cells 17-20 μ, those except in border with coarse, nodular trigones separated by thin walls; cells of vitta with strong trigones, (17) 19-24 μ wide usually, averaging 2-4 × as long as wide usually; oil-bodies smaller, 6-10 (12) per median cell, homogeneous; marginal teeth of leaves fine, regular; perianth ± obovoid to broadly obcuneate, in lateral profile, rounded at mouth, both keels winged; Appalachian. .... *P. sharpii* subsp. *sharpii*

2. Leaves oblong to obdeltoid, narrowed basally, short-decurrent antically, caducous or fragmenting, divided into several linear lobes or into 2 acute lobes (which may bear a few small teeth); leaves not vittate at base. Sectio BIDENTES. 4

4. Leaves oblong, caducous at base, bilobed (sometimes with a few small, accessory teeth); perianths little inflated except at base, with triangular teeth at mouth; without subfloral innovations. .... *P. tridenticulata*

4. Leaves obdeltoid, divided deeply into linear, fragmenting lobes, the truncate leaf-base persistent; perianth inflated, wide open at mouth, the mouth with irregular, linear caducous teeth; with 1-2 subfloral innovations. .... *P. caduciloba*

1. Oil-bodies distinctly segmented, the segments protuberant, or granular appearing and formed of minute spherules. 5

5. Leaves (in small part, at least) breaking free at their very bases; leaves rectangular to obovate: parallel-sided or narrowed from above middle to the base, narrowly inserted, short-decurrent antically and postically; never with propagula; branches all intercalary; known only from ♂ plants; shiny and ± brownish. Appalachian. Sectio CHOACHINAE. 6

6. Leaves essentially parallel-sided, on mature plants averaging over 2.0 × as long as wide, often coarsely bilobed at apex (and provided with short, ± coarse, supplementary teeth). .... *P. austini*

6. Leaves obovate, less than 2.0 × as long as wide, never bilobate, with slender, aciculate marginal teeth. .... *P. sullivantii*

5. Leaves persistent, except through mechanical injury (in *P. yokogurensis* the distal half breaking free, but the basal portion always persistent); leaves various: ovate to ovate-rotundate to ovate-oblong to rectangular, never widest above middle. 7

7. Cells large: (22) 25-40 (42) μ wide in leaf-middle; without any mode of asexual reproduction; branching normally exclusively intercalary (terminal branches absent or abnormally exceptionally present); underleaves formed of 1-several uniseriate cilia that are free virtually to base, not lamellate, vestigial. 8

8. Leaves entire or armed with numerous (12-35 usually) fine, short marginal teeth; leaves broadly ovate to rotundate to quadrate or even reniform-rotundate, from (0.8) 1.0-1.4 × as long as wide;

marginal cells of leaves not prominently elongate; oil-bodies ± coarsely segmented; dull or slightly shiny. Sectio ASPLENIOIDES. 9

9. Cells averaging (32) 34-38 (42) μ wide medially; maximal number of marginal teeth of the leaves usually 6-15. Rare or local. Perianth absent (*P. columbiana*) or entire at mouth (*P. arctica*). 10

10. Leaves rounded-quadrate, the truncate apex irregularly, shallowly lobed and armed with scattered small supplementary teeth; underleaves here and there lamellate. Piedmont of the Atlantic States. .... *P. columbiana*

10. Leaves ovate to rotund-reniform, broadly rounded at apex, the margins usually entire, rarely with scattered fine teeth; underleaves always of 2-several vestigial cilia. Arctic. .... *P. arctica*

9. Cells averaging (21) 25-32 μ wide medially; leaves varying from entire to armed with a maximum of *ca.* 25-35 fine marginal teeth. Ubiquitous. Often fertile: perianth long-emergent, closely dentate at mouth. (*P. asplenioides* and *P. satoi.*) .... See couplet 11, Key on page 98

8. Leaves armed with few (usually [3] 7-12) linear, aciculate teeth ending in mostly 4-6 elongated, superimposed cells, or with incipient bilobing at summit; leaves oblong to narrowly rectangulate to ovate, at least 1.32-2.0 × as long as wide; marginal cells, except at apex, often ± elongated; oil-bodies finely segmented; strongly shiny; cells averaging 25-32 μ wide in leaf-middle. Sectio SUBPLANAE. 11

11. Leaves narrow, oblong to rectangulate (1.65) 1.8-2.3 × as long as wide, the apices not or inconspicuously bilobed; Ozarkian. .... *P. japonica* subsp. *ciliigera*

11. Leaves ovate to oblong-ovate, 1.2-1.8 × as long as broad, the apices with incipient to marked bilobing (two of the distal teeth markedly elaborated). 12

12. Leaves with teeth slender, aciculate, formed of up to 5-6 superimposed, narrow cells; green; leaves nearly or quite flat. Southern Appalachian. .... *P. echinata*

12. Leaves with teeth sharp, variable, sometimes reduced (and then leaves merely incipiently bilobed at apex), never slenderly ciliiform, formed at most of 2-3 superimposed cells; brownish; leaves with dorsal and postical margins deflexed, thus adaxially convex. North Pacific. .... *P. rhizophora* subsp. *confusa*

7. Cells smaller: usually 18-23 μ wide in leaf-middle; leaves able to produce propagula (usually from the postical leaf-surface; these usually present on some plants in every mat, but lacking when plants growing under unusually moist conditions); teeth of leaves usually rather few (7-12, rarely to 25), rather coarse and ± broad-based, never aciculate. 13

13. Leaves postically short-decurrent, contiguously to loosely imbricate, the stem (in postical aspect) freely and *usually extensively exposed;* the short-decurrent postical leaf-base nearly flat or narrowly erect, not elevated to form a crista; underleaves normally minute, of 1-several vestigial and short cilia; perianths with postical and antical keels subequal. 14

14. Leaves uniformly persistent, ± dull; usually with very free formation of propagula; leaves ovate to rectangulate, never distinctly falcate. 15

15. Leaves contiguous to imbricate, not sharply margined; leaves in drying variously deflexed or convolute, but never becoming narrowly tubular; leaves ovate, often narrowly so, or ovate-rectangulate, always slightly dilated above postical base (in *P. floridana* not or scarcely so; this species with leaves suberect), their length (1.1) 1.25-2.0 (rarely 2.2-2.4) × their width; branches at least in part intercalary; gynoecia on leading shoots. Sectio CONTIGUAE. 16

16. Leaves, even on upper positions of shoots, widely spreading (usually at an angle of 65-75°); mature shoot-sectors with leaves so inserted that postical leaf-margins are at *ca.* (75-80) 85-90° with stem; leaves usually ovate or ovate-rectangulate, mostly 1.25-1.75 × as long as wide. Habitually sterile. 17

17. Cells slightly to distinctly collenchymatous: with thin walls, but small to coarsely bulging, sharply defined trigones; leaves distinctly ovate, usually 1.45-1.75 × as long as wide, not broadly rounded-truncate at apex; leaf-margins with dentition usually coarse and irregular. Appalachian. 18

18. Trigones in distal half of leaf minute to small, rarely weakly bulging; marginal cells, except near postical base, never set off as a thick-walled row, median cells mostly 20-25 (28) μ wide; almost always on limestone; green. ....*P. virginica* var. *virginica*

18. Trigones coarse, bulging to broadly confluent; marginal cells usually ± elongate and forming a thick-walled border; median cells (16) 18-21 (23) μ wide; rarely or never on limestone; aerial stems small, usually brownish, simple. ....*P. virginica* var. *caroliniana*

17. Cells becoming equally thick-walled, especially in several marginal cell-rows, with small trigones or almost non-collenchymatous; leaves shortly oblong to oblong-ovate, not distinctly ampliate above postical base, mostly (1.1) 1.25-1.35 × as long as wide, broadly rounded-truncate at apex; leaves with small and ± inconspicuous teeth. Coastal Plain. ....*P. aspleniformis*

16. Leaves, except occasionally at bases of old shoots, erect-spreading, usually at an angle of (40) 45-55 (65)° with stem; the leaves with postical margin clearly at an acute angle with stem (except sometimes on older stems); leaves narrowly ovate-oblong to rectangulate, usually 2.0-2.2 (2.5) × as long as wide. Often fertile. Coastal Plain. 19

19. Leaves coarsely dentate, rectangulate, almost or quite parallel-sided, rather densely imbricate, truncate at apex; leaves usually at a 40-50° angle

throughout the shoot; perianth with mouth coarsely spinose-ciliate to laciniate. ....*P. floridana*

19. Leaves finely dentate, often subentire, ovate-rectangulate, the postical base slightly ampliate, loosely imbricate, rounded or rounded-truncate at apex; lower leaves often at an angle of 55-65 (70)°; perianth mouth usually relatively short-dentate. ....*P. dubia*

15. Leaves distant, distinctly margined (the marginal cell-row with the tangential walls strongly thickened); leaves in drying narrowly, tubularly convolute; leaves parallel-sided, narrowly rectangulate, not at all dilated above postical base, their length usually 2.0-2.4 (3.0) $\times$ their width; branches copious, furcate, normally terminal; gynoecia on ultimate branches of deliquescent, decompound system. S. Florida. Sectio PARALLELAE. ....*P. diffusa*

14. Leaves, or many of them, dehiscing near the middle, leaving persistent, truncated stubs (the distal caducous portions developing propagula — usually not before dehiscence); leaves shiny when dry, when mature more or less strongly falcate. Piedmont and Coastal Plain, into the peripheral Appalachian gorges. Sectio YOKOGURENSES. ....*P. yokogurensis* subsp. *fragilifolia*

13. Leaves densely imbricate, long-decurrent (only in *P. hypnoides* short-decurrent) postically, the *stem in postical aspect quite hidden;* the postical leaf-base erect, forming a crista, or reflexed to form a water-sac; underleaves large usually, of 1-several conspicuous cilia or laciniae, or lamellate; perianth typically with antical keel much longer than postical. 20

20. Leaves postically short-decurrent (for less than 0.3 the merophyte length), regularly spinose-dentate from the $\pm$ truncate apex to near postical base; postical base slightly elevated to form a crista, never tubularly reflexed; underleaves (when normally developed) a ciliate lamella. S. Florida. Sectio HYPNOIDES. ....*P. hypnoides*

20. Leaves postically long-decurrent (for over 0.6 the merophyte length on mature leaves), the area above the postical base edentate (or else reflexed to form a water-sac); underleaves deeply divided, almost to base, into 2-several cilia or laciniae. Sectio CRISPATAE. 21

21. Leaves not strongly and regularly crispate-undulate along the postical margin; propagula usually abundantly produced; nearly restricted to Coastal Plain. 22

22. Postical leaf-base erect, forming a crista, not reflexed, edentate (or rarely with a single tooth), the distal portion of the leaf usually sharply spinose-dentate; leaves never strongly falcate; underleaves of several lanceolate to linear segments, several cells wide at base. ....*P. ludoviciana*

22. Postical leaf-base reflexed to form a tubular water-sac or pocket, its margins $\pm$ spinose-dentate; distal portions of leaves weakly dentate to virtually entire; leaves often strongly falcate; underleaves of several long cilia, 1 (2) cells wide at base. ....*P. miradorensis*

21. Leaves strongly and regularly crispate-undulate along entire postical margin; postical base, entire postical margin, and often apex, virtually or quite edentate, rarely with low, obtuse teeth; propagula rarely produced; from Coastal Plain into Piedmont and edges of the Appalachians. ....*P. undata*

TREATMENT OF SPECIES

Sectio I. Asplenioides Carl

Plants relatively robust, (2.5) 3.5-8 mm wide x 2-10 (13) cm long, green to olive-green, forming thick, extensive mats. Stem with cortex (1-2) 3-5 cell-layers thick, ± thick-walled; branching ± *exclusively intercalary, sparse, monopodial; commonly stoloniferous* from near base of lateral intercalary branches; often innovating from beneath the perianth. Leaves usually spreading laterally, often almost horizontally, sometimes deflexed, sometimes erect-appressed, imbricate to somewhat distant, varying from *suborbicular or rotund-reniform to rounded-rectangular or ovate, broadly rounded at the apex,* their length *ca.* (0.8) 1.0- 1.45 × their maximal width; leaf-margins showing variation from *edentate, with apex entire, to nearly uniformly, relatively finely dentate, with 15-35 (50)* teeth, the teeth usually (*1*) *2-5 cells long and 1-2* (*3-4*) *cells wide at base, of nearly isodiametric cells,* but the terminal cells often 2-3.5 × as long as wide, usually confined to the postical margin and apex of leaf but occasionally several on distal one-half of antical margin; antical margin straight to slightly to somewhat convexly arched, but usually not nearly as strongly so as the moderately arched postical margin; antical margin slightly to strongly recurved, the cnemis distinct but not always sharply developed, sometimes lacking; line of insertion elongate, but leaf distinctly narrowed basally, *widest some distance above base or rarely even medially* or somewhat above; *postical base exceedingly short-decurrent; the antical base moderately long-decurrent. Underleaves minute,* of a few cilia. *Cells relatively large* (25-38 μ and nearly isodiametric medially, to 38-42 x 42-50 μ), usually thin-walled and with small, occasionally bulging trigones, *near base little elongate, not forming a vitta;* oil-bodies of discrete, rather few to numerous protruding globules, *finely to coarsely segmented,* mostly 4-12 (20) per median cell (where known). *Asexual reproduction absent.*

Frequently fertile and occasionally producing sporophytes. Gynoecia terminal on leading shoots, often with innovations; archegonia usually numerous (20-25 per gynoecium). Perichaetial bracts similar to leaves in form, similarly dentate as the leaves; *perianth scapaniate*

in lateral view, ca. 1.6-2.5 × as long as wide when mature (except in *P. arctica*), strongly laterally-compressed distally, *the subequal, elongate, dorsal and postical keels subparallel except near base, not winged;* perianth-mouth dentate or entire, the teeth not or little longer than those of the leaves, the mouth often laterally recurved. *Androecia becoming intercalary, solitary,* of 4-10 pairs of bracts, compact, imbricate; bracts like leaves, but suberect with erect-spreading apices, smaller than vegetative leaves, ± denticulate like vegetative leaves.

The section includes the local *P. columbiana* and the two essentially circumboreal species, *P. asplenioides* and *P. arctica,* the oceanic *P. major* and *P. satoi,* and a doubtfully distinct third, north Pacific species, *P. ovalifolia* Mitt.

The section stands isolated among the rest of our nearctic Plagiochilae. Its species bear some superficial resemblances to those of Sectio Zonatae (*P. sharpii* complex), in leaf-form, abundant fertility, lack of asexual reproduction, dentition of leaves, but differ as follows: oil-bodies segmented; basal vitta absent; cells usually much less collenchymatous and much larger; teeth of leaves usually less coarse and tending (in many modifications) to be totally absent. The branching is essentially identical (see following paragraph). The similarities between the two sections may be largely superficial, but the similarity in perianth-form (perianths elongate, with long dorsal and ventral keels, a generally squarely truncate mouth), the total lack of asexual reproduction, the similarity in leaf-form and the tendency to produce numerous teeth of the leaves, are all very suggestive. Furthermore, the more xeromorphic forms (mod. *densifolia-latifolia-denticulata-pachyderma*) of *P. asplenioides* (= var. *devexa* Carr.) and of *P. satoi* have the leaves strongly secund postically and abaxially concave, very much as in *P. sharpii* and the majority of other species in the Zonatae. The writer would suggest that the Asplenioides stand in distinct relationship to the Zonatae.

Although terminal branches have been repeatedly searched for in the six species assigned to the Asplenioides (including *P. ovalifolia*), I have succeeded in finding terminal branches only once in *P. columbiana,* and in a collection of *P. ovalifolia.* They are particularly frequent in male plants of the latter (*Inoue* 4510; see p. 130); however, even in *P. ovalifolia* the majority of plants appear to produce exclusively, or at least overwhelmingly, lateral intercalary branches. Evidently only intercalary branches are regularly produced in the other species, and these are normally from the lower halves of the leaf-axils; a single postical intercalary flagellum has been observed. In this respect, the Asplenioides show obvious affinities to the Zonatae, in which branching also appears to be nearly or quite exclusively intercalary (at least in our species).

The ascending leafy shoots always arise as axillary branches originating near the postical base of a lateral leaf. This is also true for the frequent descending, obsolete-leaved, stoloniferous rhizoidous branches (see Fig. 10B: 2, *P. arctica*). Of some systematic significance is the fact that in the Asplenioides and Zonatae, sections which bear other striking similarities, the ascending leafy shoots often, or sporadically, produce a short distance above their origin a postically originating, rhizoidous, positively geotropic stolon (see Fig. XI: 27 in Inoue, 1958). An extreme variation of this type of branching was considered

by Carl as the primary basis for establishing the genus *Chiastocaulon*. It is evident from study of the less derivative species of *Plagiochila* that the *Chiastocaulon*-type branching can be matched almost perfectly in *Plagiochila* and therefore renders the separation of *Chiastocaulon*, as a genus, questionable. (Since the above was written, Inoue [1958] has actually reduced *Chiastocaulon* to a subgenus of *Plagiochila*.)

The taxonomy of the species of the Sectio Asplenioides is chaotic at present. Neither the present treatment nor any other that relies on study of the taxa within a single geographical area can hope to unravel the intricate relationships of the species included in the *P. asplenioides* complex. According to my interpretation, we have four basic units represented in the North Atlantic region which appear to develop vicariads in the North Pacific in two cases. These are cited, in order of increasing cell size:

Regional Representative	*Asiatic Vicariad*
1. *P. asplenioides* s. str. (median cells *ca.* 25-32 μ wide)	*P satoi* Hattori (median cells "21-30 x 25-34 μ")
2. *P. major* (Nees) S. Arnell (median cells 30-36 μ wide)	*P. "asplenioides* subsp. *ovalifolia"* (sensu Inoue) (median cells 31-41 x 37-55 μ, *fide* Inoue).
3. *P. arctica* and *P. columbiana* (median cells 34-42 μ wide; leaves edentate or paucidentate)	No known Asiatic equivalent, although *P. hakkodensis* Steph. appears to be close to *P. columbiana*.

The European and North American representatives, in general, possess the ability to produce only small marginal teeth of the leaves; the two East Asiatic taxa, in contrast, have the ability to develop coarser, sharper dentition, only *P. satoi* occasionally developing a mod. *integrifolia*.

Part of the confusion with respect to the plants of the Asplenioides lies in the misleading and often contradictory statements in the literature as to cell size. We need to immediately discount anything stated in Frye and Clark (1946) as to cell size, since these authors confused *P. asplenioides* with *P. arctica*. However, Persson (1946, p. 50), who correctly gives the differences between these two species, states that in *P. asplenioides* the median cells are 25-32 μ, in *P. arctica*, 35-45 μ. By contrast, Inoue (in lit.) assigns the cells the following dimensions: *P. satoi*, 21-30 x 25-34 μ; *P. asplenioides* s. lat. (to include *P. ovalifolia*) 31-41 x 37-55 μ. Obviously there are contradictions in these figures.

This situation is rendered more complex when the Alaskan specimens assigned in the literature to *P. asplenioides* (Evans, 1900 and 1915) are studied. The Alaskan material falls into three categories, as regards size: a large-celled extreme, clearly *P. arctica;* a medium-sized extreme, which could be referred to either *P. "asplenioides* subsp. *ovalifolia"* or to *P. major*, as regards cell size; and a small-celled extreme, which could be referred to either *P. asplenioides* s. str., or to *P. satoi*. This small-celled Alaskan extreme represents a plant whose overall size is also rather diminutive, although the plants are freely fertile. After much hesitation, I have decided to refer these plants to *P. satoi* Hattori, to which H. Inoue referred two of the Alaskan collections submitted to him. Admittedly, the status of *P. satoi* as a distinct species, and particularly, the status of the Alaskan collections referred to *P. satoi*, as distinct from *P. asplenioides*, must remain questionable. Culture experiments are much needed here.

The five regional taxa are separable by the keys to species, given earlier (pp. 97-111). The following synopsis of our species is added as orientation for the following discussion:

TABLE I—Comparative cell sizes in Sectio Asplenioides

Collections	Median Cells	Marginal Cells of Apex	Marginal Cells (middle postical margin)	Basal Cells
P. satoi				
Japanese plants (*Fide* Inoue)	21-30 x 25-34 μ	20-26 x 20-27 μ	....	27-34 x 50-80 μ
Japan Inoue 3961	25-27 (28) x 25-33 μ	(18) 19-23 (24) x 20-25 μ	(19) 20-25 x 20-25 μ	(21) 23-26 x 38-55 (75) μ
Port Alice, Alaska (Frye 724)	(21) 22-25 (27) x 24-28 (32) μ	18-21 x (18) 19-23 μ	(18) 19-22 (24) x 20-26 μ	17-21 (22) x 32-48 μ
Zarembo I. Alaska (Frye 230)	(23) 24-26 (27) x 25-28 (30) μ	(17) 18-21 x 18-23 μ	(17) 18-22 x 19-24 μ	(19) 20-24 x (40) 50-65 μ
Nichols Bay, Alaska (Frye 392a)	(23) 25-27 x 25-27 (30) μ	16-21 (22) x 17-22 μ	19-23 x 20-25 μ	(23) 25-28 x 40-50 (65) μ
P. asplenioides (European phase)				
Edwins Ford, Wales (E. W. Jones)	25-32 (33) x 25-34 μ	(21) 24-27 x 24-28 μ	24-27 x 24-27 μ	25-28 x (36) 48-60 μ
Jämtland, Sweden (Florin, 1944)	(24) 25-28 x 26-32 μ	(20) 21- 24 x 22-25 μ	(20) 21-24 x 22-25 μ	25-28 x (28) 32-45 μ
P. asplenioides (Eastern phase)				
N. Carolina Schuster 28883	(24) 25-28 (30) x 26-28 (32) μ	(18) 19-21 (24) x 24-27 μ	24-27 x 24-28 μ	24-28 x 36-50 μ
Big Creek, Ga. Schuster 40030	24-28 (30) x 25-32 (36) μ	(20) 21-26 x 23-27 μ	24-27 x 23-28 μ	(23) 24-27 x (35) 40-55 μ
N. Carolina Schuster 39372	(23) 24-26 x 25-30 μ	(19) 20-24 (25) x 22-27 μ	24-27 x 23-28 μ	(23) 24-27 x (35) 40-55 μ
Indiana Schuster 18235	25-30 (35) x 28-34 (36) μ	24-28 x 28-34 μ	25-28 x 24-33 μ	28-34 x 40-48 (58-64) μ
P. asplenioides subarctica				
Ellesmere I., Schuster 35625	23-25 (27) x 23-28 (30) μ	(16) 17-20 x 17-21 μ	....	23-28 (30) x 25-28 μ
P. asplenioides (Western phase)				
Queen Charlotte I., B.C., Persson	25-29 (32) x 32-34 μ	(21) 22-24 (26) x 23-25 (28) μ	(23) 25-29 x 24-30 μ	25-28 (35) x 55-70 (75) μ

TABLE I.—(*continued*)

Collections	Median Cells	Marginal Cells of Apex	Marginal Cells (middle postical margin)	Basal Cells
Unalaska, Alaska J. P. Anderson	29-33 x 32-36 μ	21-23 x 23-32 μ	25-28 x 24-28 μ	32-35 x 50-60 μ
Juneau, Alaska A. S. Hitchcock	29-34 x 32-34 μ	20-24 (28) x 20-28 μ	30-34 x 25-29 μ	28-32 x 54-65 μ (100-120 μ long)
Kuiu I., Alaska E. P. & E. S. Walker	30-33 (36) x 30-34 (36) μ	33-35 x 27-34 μ	30-34 x 25-34 μ	28-32 x 38-44 μ
Mt. Evans, Colo. Weber 8909	(29) 30-33 x 30-35 (38) μ	(23) 25-30 x 25-30 μ	25-32 x 25-35 μ	25-30 (36) x 35-45 μ
P. asplenioides "subsp. ovalifolia" Japan (*Fide* Inoue)	31-34 x 37-55 μ	27-37 x 31-44 μ	....	27-40 x 55-80 μ
P. ? major Annette I., Alaska (Frye 130)	(32) 33-36 (41) x 38-45 μ	25-28 (33) x 23-28 (30) μ	(25) 30-33 (35) μ	(25) 28-38 x (50) 60-75 μ (35) 36-40 x 75-85 (100) μ
Augustine Bay, Alaska (Frye 544)	30-35 (37-38) x 36-42 (48) μ	(25) 27-30 x 30-35 (38) μ	(25) 26-32 (35) x 20-25 (30) μ	32-36 x 55-75 (85) μ
St. Johns Harbor, Alaska (Frye 246)	32-36 x 35-43 μ	(25) 28-33 μ	(28) 30-33 (35) x 25-30 μ	25-28 (30) x (50) 60-80 μ
P. arctica Mt. Pullen, Ellesmere I., Schuster 35376	38-44 x 40-46 μ	(29) 30-36 μ	....	(29) 32-40 x 40-60 μ
Cape Rutherford, Ellesmere I., Simmons 669	(33) 35-45 x (35) 37-46 μ	(33) 35-44 x (30) 32-40 μ	....	(33) 35-40 x 40-50 (55) μ
Cape Rutherford, Ellesmere I., Simmons 781	(33) 35-42 x 35-42 (45) μ	(32) 35-42 x (28) 32-35 (40) μ	....	(35) 38-45 x 40-55 (60) μ
Unalaska, Alaska E. Hultén	35-39 x 48-52-60 μ	27-30 x 34 24 x 32-36 μ	42-48 x 25-34 μ	34-38 x 62-72 μ
Unalaska, Alaska E. Hultén	33-40 x 45-54 μ	34-36 x 24-30 μ	34-42 x 28-34 μ	33-36 x 55-72 μ
King Cove, Alaska W. J. Eyerdam	34-37 x 34-44 μ	28-34 x 28-34 μ	32-35 x 32-34 μ	35-40 x 45-54 μ

TABLE I.—(*continued*)

Collections	Median Cells	Marginal Cells of Apex	Marginal Cells (middle postical margin)	Basal Cells
Unalaska, Alaska W. J. Eyerdam	38-42 x 42-50 μ	30-34 x 34-45 μ	42-48 x 32-36 μ	36-40 x 46-52 μ
Unalaska, Alaska J. P. Anderson	34-40 x 36-43 μ	30-34 x 23-30 μ	34-37 x 32-34 μ	34-40 x 42-68 μ
Unalaska, Alaska E. Hultén	33-36 x 35-42 μ	32-37 x 23-28 μ	41-44 x 28-34 μ	33-35 x 34-43 μ
Unalaska, Alaska W. J. Eyerdam	34-38 x 40-44 μ	32-34 x 27-29 μ	33-36 x 24-34 μ	33-36 x 50-65 μ
Steere 17944	34-37 x 38-42 μ	29-33 x 24-30 μ	38-44 x 32-36 μ	36-45 x 48-58 (78) μ
P. arctica var. *intermedia*				
Brooks Range, Alaska, Steere 16897	33-42 (44) x 36-45 μ	23-25 x 30-37 μ	24-36 x 34-42 (48) μ	32-36 (40) x 38-50 (60) μ
P. columbiana Blomquist 7189	32-40 x 34-45 μ	32-35 x 32-38 μ	30-40 x 32-36 μ	34-37 x 45-52 μ
Blomquist 2721 N. Carolina	34-39 x 38-41 μ; 34-42 x 42-46 μ	25-35 x 25-35μ; 30-36 x 23-35 μ	24-35 x 23-35 μ; 34-46 x 23-33 μ	35-40 x 43-54μ; 35-40 x 42-48 (55) μ

SYNOPSIS OF SPECIES OF SECTIO ASPLENIOIDES

1. Leaf cells small or medium-sized: the median averaging 21-32 μ wide; marginal cells small, those lying within the marginal teeth averaging from 17-20 μ up to 20-25 μ, tangentially measured. (Perianth mouth always closely dentate to denticulate.) 2
   2. Leaf cells extremely small: the median from 21-25 x 22-26 μ up to 21-30 x 25-32 μ; marginal cells 17-20 μ up to 19-22 μ; base of leaf with very slight indication of a vitta (particularly on well-developed leaves); leaves usually nearly orbicular to broadly ovate-rotundate; dorsal margin broadly and strongly reflexed for nearly its entire length; leaves always dentate. North Pacific and Oceanic. .... *P. satoi*
   2. Leaf cells medium-sized: the median 25-32 (33) μ wide x (28) 30-36 μ; marginal cells near apex (20) 21-25 (28) μ; base of leaf never obscurely vittate; leaves very variable in shape, entire-margined to dentate, the antical margin moderately to slightly reflexed; very widespread. .... *P. asplenioides*
1. Leaf cells large to very large: the median averaging 32-36 μ wide x 35-40 μ long or more; marginal cells 25-36 μ or larger, tangentially measured. (Leaves never with a trace of basal vitta.) 3
   3. Leaves ovate to rotundate-reniform, never bilobed; leaves regularly and finely pluridentate or entire-margined; branching exclusively intercalary; Arctic or Oceanic. 4

4. Leaves laterally patent, usually freely denticulate; cells somewhat smaller: the median 32-36 (37) μ wide; leaves ovate in shape, always longer than broad; perianth longly emergent, denticulate at mouth. Oceanic and suboceanic; robust. ....[*P. major*]
4. Leaves usually erect or suberect, often erect-connivent and appressed, entire-margined or rarely obscurely and obsoletely denticulate; cells very large: the median (34) 35-42 μ wide x (38) 40-48 (50) μ long; leaves usually broadly reniform-rotundate, usually broader than long; perianth slightly or not emergent, the broadly truncate mouth entire. Arctic; usually small. ....*P. arctica*
3. Leaves quadrate-rotundate, shallowly and asymmetrically bilobed at apex and with a few minute accessory teeth; with occasional terminal branches; uniformly sterile; cells as in *P. arctica*. Piedmont of SE. United States. ....*P. columbiana*

Of the five taxa in the preceding key, the occurrence of *P. major* in North America is doubtful. I have included a diagnosis and discussion of the species (pp. 143-146), and questionably refer several Alaskan individuals to it. No specimens even approaching the very robust European *P. major* have been seen from North America.

The discrepancies in cell-size between the American and European members of some species, *vis a vis* their Japanese counterparts, are noteworthy (Table I). For example, *P. asplenioides* var. *subarctica* has cells no larger than in *P. satoi.* Similarly, the Alaskan plants of the *P. asplenioides-major* Complex have cells consistently larger than those of typical, Eastern American *P. asplenioides,* but roughly equivalent in size to the Japanese plants assigned by Inoue to *P. asplenioides* subsp. *ovalifolia.*

PLAGIOCHILA ASPLENIOIDES (L.) Dumort.

Figs. 7:9-13, 8, 9, 10A, 13

Jungermannia asplenioides Linnaeus, Sp. Pl. 1131, 1753.
Candollea asplenioides Raddi, Mem. Soc. Ital. Sci. Modena 18:11, 1818.
Jungermannia viticulosa Schweinitz, Sp. Fl. Amer. Hep. 14, 1821, (not of Linnaeus, Sp. Pl. 1597, 1753).
Radula asplenioides Dumortier, Comm. Bot. 112, 1822.
Jungermannia porelloides Torrey ex Nees, Naturg. Eur. Leberm. 1:170, 1833.
Plagiochila asplenioides Dumort., Rec. d' Obs. 14, 1835.
Plagiochila porelloides Lindenberg & Gottasche, Sp. Hep. 61, pl. 12, 1839?
Jungermannia dillenii Taylor, Trans. Bot. Soc. Edinburgh, 2:316, 1846.
Plagiochila nodosa Taylor, London J. Bot. 5:268, 1846.
Plagiochila dillenii Taylor, *ibid.* 5:261, 1846.
Plagiochila porelloides var. *nodosa* Pearson, Geol. Natur. Hist. Surv. Canada, Ser. 3, List of Canadian Hepaticae 19, 1890.
Plagiochila arctica Frye & Clark, Univ. Wash. Publ. Biol. 6(3):435, 1944 (not of Bryhn & Kaalaas, 1906).

Plants generally in large patches or mats, more rarely creeping among other bryophytes, yellowish-green (when in sun) to pure or deep green to somewhat dull, olive green, the *leaves never brownish* (but stems often brownish), usually quite *dull. Plants excessively polymorphic,* varying from 1.8-6 mm wide and 1-10 cm long, with

diffuse monopodial branching. Stems *ca.* 250-500 μ thick, occasionally thicker; cortex usually 2-4, occasionally 5 cell-layers thick, the cells smaller than the medullary, more or less thick-walled, often brownish to yellowish. Rhizoids absent on mature aerial branches, but often frequent on the decumbent leafy shoots of reduced, impoverished forms. Leaves varying from laterally patent to spreading but strongly secund postically, to ± flat and erect-appressed, distant to moderately imbricate, their insertion moderately acroscopically arched, slightly to moderately decurrent dorsally, *very short decurrent* (less than 0.2 the merophyte length) *postically,* basically *broadly ovate to subovate in shape, widest a short distance above the somewhat narrowed base* (but in *reduced forms with leaves suborbicular* to short- rectangular-rounded, widest near middle), *their length ca. 1.2-1.5 × their width,* usually 1.8-4 mm long x 1.3-3.5 mm wide; cnemis poorly to moderately developed, the antical margin reflexed for most of its length (in luxuriant shoots) to scarcely reflexed (in impoverished plants); *leaf-margins typically with 18-32 small and regular sharp marginal teeth,* the teeth varying from 1-celled to 2-3 (4) cells long, but *in most impoverished forms subentire;* leaves usually spreading at an angle of 60-80 degrees with stem, more or less postically deflexed. Juvenile leaves, and leaves of impoverished plants often fully as wide as long, often retuse, emarginate, or shortly bilobed distally (with few or no other teeth). Cells more or less thin-walled, except 1-4 rows of marginal cells often thick-walled, with minute concave trigones to moderate, slightly bulging trigones; *median cells ca.* 25-30 (34) μ x 30-35 (36) μ, nearly isodiametric, *near margins* (22) 25-29 (32) μ, scarcely elongate, the walls thin or slightly thickened; cells scarcely wider at middle of base, there to 28-34 (36) x (35-38) 40-50 (60) μ long; oil-bodies usually 3-8 (9-12) per median cell, up to 16-21 in a few basal cells, *distinctly segmented* and of relatively few coarse (2-3 μ) to moderately numerous smaller (less than 1 μ) globules, which protrude individually, varying from 3 x 5 to 4 x 6 to 4-5 x 9-10, rarely 6 x 9-12 μ; cuticle sometimes appearing finely punctulate. *Underleaves minute,* inconspicuous, filiform to 2-3-4 multifid, *of ciliary segments. Asexual reproduction quite absent.*

Male and female plants usually in separate patches. Male plants often showing slight heterothalism and somewhat smaller than female plants from the same site. Androecia solitary, at first terminal, eventually always intercalary, spicate, compact, of 5-10 pairs of closely imbricate bracts, usually somewhat yellowish or whitish-yellow (in obvious contrast to the green leaves). Bracts similar to leaves, but strongly ventricose, suberect, except for the distal one-fourth, which is erect-spreading to spreading; margins entire to subentire, often denticulate like leaves; bract length *ca.* 1.5, width *ca.* 1 mm; antheridia usually 2-3. Female inflorescences terminal, often with 1-2 subfloral innovations. Bracts dentate like leaves but usually somewhat wider; in many cases the vegetative leaves entire, but the bracts and subfloral several pairs of leaves progressively more distinctly denticulate. Perianth

elongate, to 5-7 mm long, *ca.* 2-2.5 × as long as wide at mouth, the dorsal and ventral keels sharp distally, but not winged, entire; mouth strongly laterally compressed, often reflexed, finely dentate like leaf-margins (but often more coarsely so, and somewhat ciliate-dentate); mouth with truncation at right angles to stem, not or hardly oblique, the dorsal and ventral keels subequal.

Sporophyte infrequent. Seta of many cell-rows, *ca.* 350-400 μ in

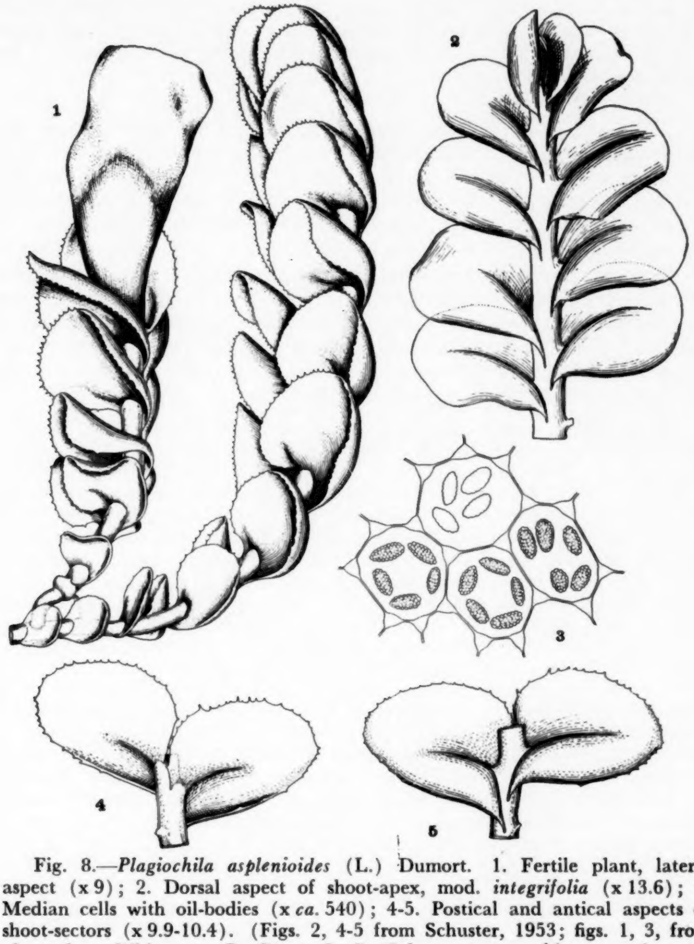

Fig. 8.—*Plagiochila asplenioides* (L.) Dumort. 1. Fertile plant, lateral aspect (x 9); 2. Dorsal aspect of shoot-apex, mod. *integrifolia* (x 13.6); 3. Median cells with oil-bodies (x *ca.* 540); 4-5. Postical and antical aspects of shoot-sectors (x 9.9-10.4). (Figs. 2, 4-5 from Schuster, 1953; figs. 1, 3, from plants from Whitewater R. Gorge, S. C., *Schuster,* approaching var. *devexa*).

diam., to 5 cm long, the epidermal cells in up to 45-50 rows, somewhat or scarcely smaller in size than interior cells. Capsule short-ellipsoid, *ca.* 1.5-2 mm long; wall 7-8 cell-layers thick. Spores usually (15) 16-18 (19) μ; elaters *ca.* 7-8 (9-10) μ in diameter, bispiral. Chromosome no. = 9.

Müller (1956, p. 893) states Lorbeer obtained, by apospory, a diploid race with 18 chromosomes. In this the cells of the leaf-apices averaged 33-40 μ and the median cells averaged 33 x 45-60 μ. Is it possible that *P. arctica* and *P. major* arose this way? Müller also incorrectly states the seta is only 1-2 cells thick. He described the outer cells as 33 μ in diam., the more thin-walled interior cells as 65 μ; the latter supposedly disintegrate at maturity, but I find them persistent.

Type.—European.

Distribution.—The most widespread species of *Plagiochila,* with a presumably holarctic distribution. In Japan replaced by the "very polymorphous" *P. ovalifolia* Mitt., which is "closely related to," and perhaps a subspecies or variety of the very common *P. asplenioides* (Hattori, 1952, p. 22). *P. asplenioides* occurs throughout most of Europe, and much of northern North America, southward only slightly into the southeastern Coastal Plain and to California and Arizona. In North America the northern range is still imperfectly known, since in the past the species was much confused with the closely allied *P. arctica.* The following represent literature reports (with pertinent citations) and collections seen (with ! marks); for the sake of brevity, collectors and numbers are generally omitted:

ELLESMERE ISLAND: edge of polar ice cap, 1.5-2 mi. W. of tip of Cape Belknap, 82°32′ N., 62°21′ W. (*Schuster* 35750, 35625; var. *subarctica*). GREENLAND: *fide* Bryhn (1906). MELVILLE PENINSULA: Vansittart I. (Polunin, 1947). NORTH BAFFIN: Pond Inlet (Polunin, 1947). NORTHWEST TERRITORIES: Belcher Isls. (Schuster, 1951). QUEBEC: Richmond Gulf (Schuster, 1951); Montreal and Mont Saint-Hilaire; Mont-Rolland; Mont Orford; Waterloo; La Tuque; Saint-Fabien Lake Mistassini; Percé, etc. (Lepage, 1945); Mt. Lac des Cygnes (Kucyniak, 1947); Bic, Rimouski Co.!; Tadoussac!; Rimouski, Rimouski Co. (*Lepage* 529!); St. Anne, Kamouraska Co. (*Lepage,* 540!); Îlot à Canuel, Rimouski (*Lepage, 1940!*) in herb. Yale as *P. arctica,* cited and figured as such in Frye and Clark, 1944. LABRADOR: no loc. (*Allen* 34!); no loc. (*Waghorne* 15!); Esquimaux River (*Allen, 1882!*). NEWFOUNDLAND: NE. Coast!; Bay of Isles!; Bay Bull's Arm! (*Waghorne,* as *P. interrupta!*); Blaketown! (*Waghorne,* as *P. interrupta!*); Placentia Bay!; Broad Cove!. NOVA SCOTIA: Yarmouth! Annapolis! Cape Breton I.! Truro; Margaree; Halifax Co. ("forma laxa") (Brown, 1936); Valley of Barrasois R., Cape Breton (*Nichols* 1447!). ONTARIO: Paradise Bay, Lake Timagami! Gull L. Portage, L. Timagami (*Cain* 1187!, 2484!); Spawning Lake Portage, Lake Timagami (*Cain* 1133!); Kokoko Bay, L. Timagami (*Cain* 2436!); Ottawa! Belleville, Owen Sound; Algonquin Park; Sudbury Jct.; Current R., Thunder Bay (Macoun, 1902). PRINCE EDWARD I.: Cove Head. NEW BRUNSWICK: Woodstock!; Queens Co.: Cannan Forks; Campobello (*Farlow, 1898!*). MAINE: Foot of Mt. Katahdin (*Schuster!*); Mt. Desert I.!; Buckfield!. NEW HAMPSHIRE: Cornish, Sullivan Co.! Tuckerman's Ravine and Hermit Lake, Mt. Washington!; Mt. Monadnock!; Mt. Lafayette, Franconia Mts.! Crawford!

VERMONT: Stratton!; Newfane!; Mt. Mansfield!; Wardsboro! MASSACHUSETTS: Malden! Purgatory, Dedham!; Cambridge!; Hazelwood!; Mt. Greylock!; Worcester; Leicester; Bash Bish Falls, Berkshire Co. (*Burnham,* 1908!); Mt. Toby, Sunderland!; Roaring Brook, Leverett!: RHODE ISLAND: Che-

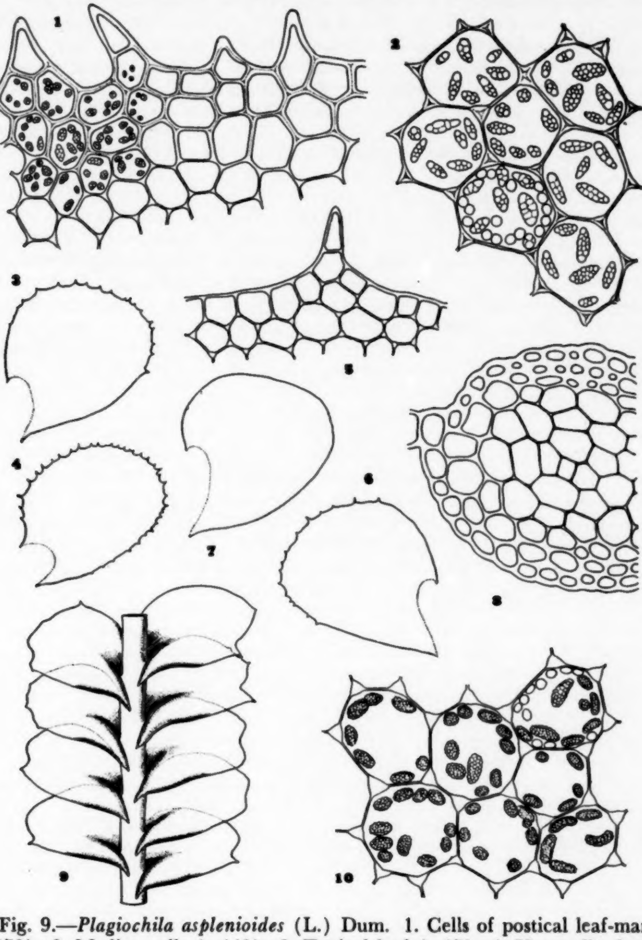

Fig. 9.—*Plagiochila asplenioides* (L.) Dum. 1. Cells of postical leaf-margin (x 270); 2. Median cells (x 440); 3. Typical leaf (x 17); 4. Unusually dentate leaf (x 13); 5. Cells of margin of leaf in fig. 6 (x 170); 6. Leaf of sparingly dentate phase (x 14); 7. Leaf of edentate phase (x 14). *P. asplenioides* var. *obcampanulata* Schuster. 8. Stem cross-section (x 160); 9. Shoot sector, showing the frequently bilobed leaves (x 9); 10. Cells from leaf of plant in fig. 9 (x 400).

pachet (Burlingame, 1894!). CONNECTICUT: West Hartford!; Sargent's R., New Haven!; Spruce Glenn, New Haven!; see also Evans and Nichols (1908). NEW YORK: Whiteface Mt.! Devil's Den, W. of Watervliet, Albany Co.!; S. base, Sugar Loaf Mt., Washington-Warren Co. line!; E. of Pattens Mills, Washington Co.!; Glenmont, S. of Albany!; Sam's Point, Ulster Co.!; Pompey!; Brewerton!; Lake Placid! Cascadilla Creek, Ithaca!; Seneca Glen, Canandaigua Lake!; Little Moose Lake, Herkimer Co.; see also numerous reports in Schuster, 1949; N. slope of Slide Mt., *ca.* 1 mi. E. Winnisook Lake (*Schuster* 17663); *ca.* 2000-2200 ft., Wittenberg Mt. (*Schuster* 24695, 24401); spruce fir forest between Cornell and Slide Mts. (*Schuster* 17584); Peasleeville, 1800-2000 ft. (*Schuster,* 1945); Yates Co., N. of Middlesex (*Schuster,* 1944); near summit, Ellenburg Mt. (*Schuster* A-244). NEW JERSEY: Palisades (*C. F. Austin, 1862!*); Closter (*C. F. Austin, 1861!*). PENNSYLVANIA: University Spring (*C. F. Austin, 1872!*); Delaware Water Gap!; near Stroudsburg!; Sayre!; also Alleghany, Bedford, Warren, Potter cos., etc. MARYLAND: Baltimore! WEST VIRGINIA: Cheat Mt., Randolph Co.; Calhoun, Clay, Gulmer, Grant, Kanawha, Marion, Marshall, McDowell, Monongalia, Pocahontas, Preston, Ritchie, Wetzel, Wirt cos. (Ammon, 1940); Shenandoah Mt., E. of Brandywine (*Schuster!*). VIRGINIA: Smyth Co., at Nicks Creek!; Buck Hollow Trail, Rappahannock Co.!; "in sylvaticis montosis" (Sullivant, Musci Allegh., 1845!); Pine Mt. near "Tentdale"!; Mt. Lake, Giles Co.!; Bull Run Mts.! also Greensville, Albemarle and Smyth cos. (Patterson, 1949, 1951); *ca.* 4200 ft., on Mt. White Top, Smyth Co. (*Schuster* 38052, 38052a, with *Lejeunea lamacerina*). NORTH CAROLINA: Macon, Jackson, Mitchell, Swain, Haywood, Ashe, Burke, McDowell, Buncombe, Alleghany, Transylvania, Caldwell, Polk cos. in the Mountains (36 specimens!); Orange, Durham, Wake, Randolph, Forsyth, Rowan, Davidson cos. in the Piedmont (18 specimens!); Hemlock Bluff near Cary, Wake Co. in Coastal Plain (*Schuster*); Andrews Bald, SW. of Clingmans Dome, Smoky Mt. Ntl. Park (*Schuster* 39750); branch from Fork Ridge, just above jct. with W. Fork Pigeon R., 4500-4600 ft., N. of Beech Gap, S. of Sunburst, Haywood Co. (*Schuster* 39374); Chattooga R., at the Narrows and at the bridge 1-1.5 mi. below Narrows, Macon and Jackson cos. (*Schuster* 39480, 39432, 39810, p.p., with *P. sharpii, P. caduciloba, Radula obconica, Lejeunea lamacerina gemminata* and *Lophocolea nuricata;* on shaded damp rock); Chattooga R., just above Ellicott Rock, barely N. of Georgia-South Carolina state lines in Jackson Co. (*Schuster and Bryan* 39811); Devil's Courthouse, on Blue Ridge Parkway W. of Wagonroad Gap, 5500 ft. (*Schuster and Bryan* 39219). TENNESSEE: Sevier, Morgan, Campbell, Rutherford, Carter, Marion, Blount cos. (18 specimens!); near Clarksville, Montgomery Co. SOUTH CAROLINA: Estatoe Creek ravine, Pickens Co. (*Schuster* 37676, 37685); Oconee Co., gorge of Whitewater R., below Lower Falls, *ca.* 4-5 mi. NW. of Jocasee (*Schuster* 25161); Chattooga R., E. side, below Ellicott Rock, Oconee Co. (*Schuster and Bryan* 39901). GEORGIA: Stephens Co.!; Dade Co. (Carroll, 1945); Chattooga R., W. side below Ellicott Rock, Rabun Co. (*Schuster and Bryan* 39831); Big Creek, just below High Falls, N. Rabun Co. (*Schuster* 40030; a delicate, but robust mesic phase, somewhat shiny when dry and relatively pale green in color; near the typical phase). OHIO: Columbus (*Sullivant, 1842!*); Laurel Falls, Adams Co. (*Fulford, 1932!*). INDIANA: Greencastle! Fern, Putnam Co.! Turkey Run State Park!; Lawrence Co. ILLINOIS: Tonti Canyon, La Salle Co.!; Jackson Co. (Hatcher, 1952). KENTUCKY: Carter!, Letcher, Lewis!, McCreary, Perry and Powell cos. (Fulford). MICHIGAN: Alger, Gogebic, Luce, Keweenaw, Emmet, Mackinac, Cheboygan cos. (12 specimens!); Lellanau, Chippewa cos.; Ann Arbor!; Deer Lake, W. of Munising, Marquette Co.! WISCONSIN: Dells of the Wisconsin!; Sauk, Villas, Oneida, Bayfield, Ash-

land, Adams, Iron, Douglas, Barron and Grant cos. (Conklin). MINNESOTA: Carlton, Cook, Lake, Lake of the Woods, Chisago, St. Louis, Stearns, Wabasha, Winona cos. (see Schuster, 1953; 57 specimens!). IOWA: Dutch Lake, Iowa Co.!; Kronk's Bluff, Montour, Tama Co.!; also, Emmet, Winnebago, Winneshiek, Allamakee, Mitchell, Fayette, Clayton, Story, Hardin, Delaware, Linn, Jones, Marion, Muscatine cos., etc. (Conard, 1945); Ledges Park, Boone Co. (Shimek, 1927). MISSOURI: E. of Oetters, Franklin Co.!; SW. of Schluersburg, St. Charles Co.!; W. of Foley, Lincoln Co.! ARKANSAS: "Lost Valley," 2 mi. NE. of Boxley, Newton Co. (*Iltis and Moore 4204!, Anderson 12161, 12164!*); Buffalo State Park, Marion Co. (*MacGregor* 5422!, 5425!); Alum Fork, W. of Benton, Saline Co. (*Anderson* 11310!); Washington Co.: Howard's Bluff E. of Springdale (*Anderson* 12262a!, 12237!). Mt. Judea (*Emig, 1913*); Boston Mts., Swain (*Emig, 1913!*).

The species also occurs in the Rocky Mountains and in the Far West, as follows:

ALASKA: Shipley Bay (*Frye* 778!; plants robust; xeric form; leaves suberect, their adaxial faces nearly pressed against stem; median cells *ca.* 28-34 μ; marginal cells 21-24 μ; median cells with bulging trigones; marginal 2-3 cell rows thick-walled; an extreme form, but not referable elsewhere); Adak I. (Stair, 1948); Excursion Inlet; Yakutat Bay; Unalaska (*fide* Clark and Frye, 1949); Farragut Bay, Sitka, near Yakutat (Evans, 1900); Hidden Inlet; Lake Bay; Swifts Cannery (Evans, 1915); Juneau; Wrangell, Baker I. (Clark and Frye, 1942); Umiat and vicinity, Colville R., approx. 69°23′ lat. N., 152°10′ W. Long. (*Steere* 17108!); Driftwood Camp, near headquarters of Utukok R., N. slope of De Long Mts., Brooks Range, approx. 68°53′ N. Lat. 161°10′ W. Long. (*Steere* 16679!); Nitrofania Bay (*G. B. Rigg* 1219!); Area between Mt. Araga and Smith Lakes, just W. of Etivluk R., Endicott Mts., Brooks Range, *ca.* 68°43′ N., 156°30′ W., 2000 ft. (*Steere* 17933! and ?17859!; also 18063!; mixed with *Radula prolifera, Tritomaria quinquedentata, Mesoptychia sahlbergii*); SW. of Chandler Lake, Endicott Mts., Brooks Range, *ca.* 68°12′ N., 152°47′ W., 3000 ft. (*Steere* 18244! 18235!; with *Diplophyllum taxifolium* and *Scapania crassiretis,* the latter new to North America!). [All of the preceding reports, except for the collections examined are doubtful; at least in part the reports of Evans (1900, 1915), Stair (1948), Clark and Frye, (1942) appear to belong to *P. satoi, P. major* or possibly *P. arctica* var. *intermedia.* Those collections, reported by the previous authors, which have been examined and found to be large-celled, are cited elsewhere under *P. major.*]. BRITISH COLUMBIA: Burrod Inlet!; Queen Charlotte Isls. (*H. Persson, 1957!*; near *P. major*); Columbia R. above Revelstoke (*Macoun,* Can. Hep. 87!) Revelstoke!; Selkirk Mts.!; Comox, Vancouver I.!; Goldstream and Departure Bay, Vancouver I. (*Macoun, 1908!*); Ucluclet (*Macoun, 1909!*); Shushwap Lake (*Brinkman, 1909!*). ALBERTA: Banff!. WASHINGTON: Pyallup!; Lake George Trail, Mt. Rainier Ntl. Park, Pierce Co.!; Paradise Valley, Mt. Rainier (*Flett!*); Elwah R. Valley, Olympic Mts., 2500 ft. (*Frye!*); near Ronald (*Clark!*). OREGON: Oneonta Gorge, 36 mi. E. of Portland (*Frye!*); Mt. Hood, 2000 ft. (*Frye!*). MONTANA: Columbia Falls!. IDAHO: Kootenai Co. (*Underwood and Cook,* Hep. Amer. No. 91!); White Crown Gulch, Moscow Mt. (*Clark!*). COLORADO: Longs Peak, Rocky Mt. Ntl. Park, 10,100 ft.! and 11,100 ft., at timberline!; Pike's Peak, 7,000-10,000 ft.!; Clear Creek Co., S. shore of Summit Lake, Mt. Evans, 12,800 ft. (*Weber* 8909!. with *Scapania hyperborea*). NEW MEXICO: Monument Peak, Santa Fe Canyon (*Arsène!*); Pinecrest, Gallinas Canyon, 8000 ft., Las Vegas (*Arsène, 1936!*); ARIZONA: Mt. Lemon, Catalina Mts., 9000 ft. (*Johnson! Bartram!*); Rincon

Mts., 8000 ft. (*Blumer!*). CALIFORNIA: Deer Creek Canyon, Humboldt Co.!, Blue Lake, Humboldt Co.!; Meadow Valley near Quincy, Plumas Co. (*Head!*); near Shasta Springs (*Eastwood!*).

There are also reports from Mexico (Gottsche, 1863), from which material has not been seen. The species is widespread in Europe, ranging southward to the Mediterranean and into North Africa. Over 450 North American collections have been examined. The report of the species from Florida (Müller, 1951-56) is incorrect.

Although there are several reports from Asia, none of the Asian specimens I have examined can be safely referred to *P. asplenioides*. A plant from Kashmir (Y) is indeterminable. The report from Japan (Mt. Tsurugi, Shikoku, Stephani, 1897, p. 81) is questioned by Hattori (1952, p. 21); I have also studied a specimen from Japan (Mt. Hyachine, Prov. Morioka, *Faurie* 1689), determined by Stephani as *P. asplenioides* (Y) which represents a species of the Zonatae, judging from the vittate leaf-base; it surely is not *P. asplenioides*.

Occurrence and Ecology.—Concurrent with the extreme variability of this ubiquitous and abundant species, we find wide variations in mode of occurrence. The plant ranges from an xeric extreme (relatively rare) to mesic and hygric forms (most frequent), with very rarely hydric, submerged forms developed.

The species occurs most often on mineral substrates, and is most common on moist rocks (usually on their vertical faces). In such situations it persists until dense sods are formed, which accumulate fine dirt particles, resulting in a dense sod of the species, with the primary stems sunken in a thin soil layer over the rock surfaces. Under such conditions the species occurs in large luxuriant masses.

In the writer's experience, it is usually not strictly a pioneer on bare rocks (quite unlike the majority of other North American species of the genus). Where it occurs on rocks, it either spreads out from initial colonies in soil-filled crevices, or else invades after preparation by pioneer species (such as those of *Marsupella* or *Scapania nemorosa*), with which it then comes into active competition. A typical example of this situation is offered by prevailing conditions in the Piedmont of North Carolina. Here on the bare vertical rock-walls (along streams) *P. yokogurensis* subsp. *fragilifolia* and *P. undata* are the pioneer species of the genus; if the rocks have a low slope, leading to accumulation of soil (or if a slight talus layer of soil builds up at their bases), we find *P. asplenioides* undergoing ecesis — but not if the rock is absolutely bare. In that area, *P. asplenioides* "behaves" almost like *P. columbiana* (and sometimes occurs with it), invading banks below cliffs and ledges, or soil-covered rocks. However, *if* moisture conditions are higher (as in humid, shaded ravines), *P. asplenioides* is able to invade more nearly bare rock surfaces. The critical factor here appears to be moisture — with, in drier areas (or areas with more intermittent moisture conditions), the species confined to moisture-retaining sites, such as soil, while in exceedingly humid sites (as near waterfalls), the species can undergo ecesis under more nearly pioneer conditions.

In our region it is almost equally at home over calcareous rocks (pH 6.8-7.0), or over acidic, igneous rocks (pH 4.5-5.5, sometimes less). Seven pH measurements from diorite and sandstone run as follows: 4.7, 4.8, 4.9, 5.4, 5.8, 6.1, 6.2. Unlike many other species (such as *P. sharpii, P. caduciloba, P. austini*), *P. asplenioides* tolerates

high insolation when moisture conditions are optimal enough, but does not produce brownish pigmentation under such conditions, though it may turn a yellowish color.

More infrequently we find the species on shaded, soil-covered banks, away from rocks; still more rarely it occurs around the bases of trees, and may actually grow 1-2 ft. up the bases of trees (after the growth of other species has resulted in accumulation of a thin humus layer). *P. asplenioides* is only exceptionally found on bark at the bases of trees (Lick Brook, Ithaca, N.Y. *Schuster* H 3453; on *Betula lutea*).

Associated with the extraordinary ability of the species to undergo ecesis in diverse habitats, we find it associated with an extremely wide range of other Hepaticae. This list is so large that, in the aggregate, it includes nearly half of the Hepaticae occurring in eastern North America.

Not only does *P. asplenioides* possess a wide ability to adapt itself to diverse edaphic conditions, and to wide fluctuations in moisture and light, but it is also able to tolerate a wider fluctuation in temperature conditions than any other species of the genus. As a consequence, it is found from arctic and alpine situations (as far north as northern Ellesmere and Alaska) southward into the Lower Austral, where it may occur with such congeneric taxa as *P. caduciloba* and *P. undata.* The species occurs here in areas where the measured temperature never falls (at soil level) below 27-28°F., and where there are up to 100 inches of rainfall per year.

At the opposite extreme is the occurrence under high arctic conditions, along the shore of the frozen Arctic Sea, northward to within 518 miles of the North Pole (NE. Ellesmere Island, *Schuster* 35625), where the species occurs as a yellow-green, densely caespitose, deviant variant (var. *subarctica,* see p. 138) over calcareous clay-shale slopes fed by permanent snow-banks. Associated here, in a very attenuated moss-tundra are several high-arctic Hepaticae (*Cryptocolea imbricata, Lophozia pellucida, L. quadriloba, L. heterocolpa* var. *harpanthoides, Cephaloziella arctica, Scapania gymnostomophila, Solenostoma polaris,* etc.) and such typical angiosperms as *Saxifraga caespitosa* and *oppositifolia, Papaver radicatum,* with the only woody plant *Salix arctica!* The growing season (1955) lasted here only from *ca.* June 25 to August 28! Precipitation averages below 4-5 in. per year, and the maximal air temperatures are *ca.* 56-60°, attained once or twice a year, with the average temperature during the two-month growing season about 32-36° F! Certainly very few species of Hepaticae show such a fantastically wide toleration for extremes in environmental conditions.

Höfler has experimentally demonstrated that *P. asplenioides* s. lat. (including *P. major*) consists of races exhibiting extraordinarily wide tolerances to desiccation (see Schuster, 1957). The large and delicate "var. *major*" (= *P. major*) was unable to tolerate desiccation to a point below 70 percent relative humidity; the small xeromorphic modification or race, "var. *minor*" was able to survive desiccation to 15-20

percent relative humidity. Schuster (1957) discusses the implications of these results in some detail. Such data clearly substantiates the field experience of the writer, who has found an extremely wide variability in *P. asplenioides* as regards toleration of several environmental factors.

Differentiation and Relationships.—*P. asplenioides* bears a good deal of resemblance to four other species of the genus occurring in our area: *P. columbiana, P. sharpii, P. satoi,* and *P. aspleniformis.* Considerable material has been seen in herbaria, of *P. asplenioides,* determined as one or the other of the three former species. In addition, a number of specimens have been seen which have been erroneously referred to *Pedinophyllum interruptum.* The leading points by which these taxa can be separated from *P. asplenioides* will be summarized below. These species, it must be stressed, are not all close to *P. asplenioides,* except *P. satoi* and *P. columbiana.* It was believed for some time, that the latter might be a peculiar polyploid race of *P. asplenioides,* limited to the Piedmont. Dr. Virginia Bryan attempted to make somatic chromosome counts of *P. columbiana,* but the material was unsuitable for an accurate count. However, it is certain that this species does not have as many as 18 chromosomes, hence cannot very well be a polyploid of *P. asplenioides.*

Much closer to *P. asplenioides* is the east Asiatic *P. ovalifolia* Mitten (Trans. Linn. Soc. London, Ser. 2, III: 193, 1891; for a full synonymy see Hattori, 1944, p. 59). Indeed, *P. ovalifolia* appears to differ only quantitatively from *P. asplenioides* in (a) the often somewhat fewer, coarser and often slightly, less equal, marginal teeth; (b) the evident inability to produce wholly entire-margined leaves; (c) the obliquely terminated perianth, often more deeply incised on the ventral side. Mitten (1891) separated the species from *P. asplenioides* on this last basis. In addition to the tendency for the perianth-mouth to be oblique, *P. ovalifolia* also differs in the tendency for the perianth-mouth lobes to be coarsely toothed, and occasionally to be again slightly bilobed or emarginate.

Since the above was written, Inoue has reduced *P. ovalifolia* to the rank of a subspecies of *P. asplenioides,* calling attention to most of the preceding differential features. He also indicates that *P. ovalifolia* has a less developed cortex, only 2-3 cells thick, *vs.* 3-5 cells thick in *P. asplenioides.* This difference does not hold when we study the Arctic phase, *P. asplenioides* var. *subarctica,* which may have a 1-2-stratose cortex. Similarly, Inoue states that *P. ovalifolia* has a tendency to develop "slightly bilobed" leaves, while in *P. asplenioides* there is supposedly "never . . . any suggestion of bilobing." However, *P. asplenioides* var. *obcampanulata,* which see, shows a marked tendency to develop incipiently bilobed leaves. In spite of the fact that two of the features supposedly unique to *P. ovalifolia* also recur sporadically in *P. asplenioides,* I still believe that the variation-patterns of the two taxa are sufficiently distinctive as to warrant the retention of two species. It is possible that the Alaskan plants, with larger cells than "normal" *P. asplenioides* (thus approaching *P. major,* under which they are tentatively cited) may represent a transition from *P. asplenioides s. str.* to *P. ovalifolia.* At any rate, *P. ovalifolia* is stated, by Inoue, to have leaf-cells considerably surpassing in size those of "normal" *P. asplenioides* (compare Table I). The variability of *P. ovalifolia* is well-

indicated by Figs. VI-VIII in Inoue (1958). It is noteworthy that although leaves similar in shape to those of typical *P. ovalifolia* and of fo. *magna* recur in *P. asplenioides,* nothing even remotely similar to the leaf-form and dentition exhibited by *P. ovalifolia* fo. *thylimanthoides* and var. *miyoshiana* are ever found in *P. asplenioides.* In short, the disparate variation-patterns of the two species, in leaf-shape, dentition, perianth-form, and cell-size suggest that there is a large enough ensemble of genetic differences between them as to prohibit our considering them to be identical species. It is furthermore, desirable to keep these two taxa separate in order that the variability of *P. asplenioides* not be broadened to the point where comprehension becomes impossible; see p. 130.

The other closely allied taxa in the *P. asplenioides* complex are *P. arctica,* a high-arctic derivative with much larger leaf-cells (see p. 146), *P. major,* a largely oceanic derivative of much more robust size and with somewhat larger leaf-cells (see p. 143), the Formosan *P. magnifolia,* which is the most vigorous species of the group and bears the largest leaf cells (see p. 146). Also closely related is the polymorphous *P. delavayi* Steph. from China, a plant that Carl (1931, p. 101) suggests may be a mere geographical race of the ubiquitous *P. asplenioides,* and the North Pacific *P. satoi* (see p. 154).

The polymorphism of *P. asplenioides* has led to so much confusion with other, relatively remotely allied taxa that the differentiation from potentially confusing species is dealt with at some length, as follows:

1. Confusion with *Pedinophyllum interruptum* (see under *Pedinophyllum*).

2. Confusion with *Plagiochila columbiana:* Occasional forms of *P. asplenioides* (as, for instance, less robust plants of *Schuster* 25236, Dry Falls, N. C.) show subentire leaves, emarginate at the apex, less than 1.4 × as long as wide, with the lower leaf-lobe often spiniform, the upper larger and broader, often broadly rounded (Fig. 9:9). Such forms further agree in that (in addition to the two shallow lobes) occasional small marginal teeth, irregularly distributed, occur. Such plants are habitually inseparable from *P. columbiana.* They can be separated most readily from the latter by the smaller leaf-cells (up to 26-33 μ in the leaf-middle *vs.* 36-42 μ in *P. columbiana*).

3. Confusion with *P. sharpii:* The mod. *denticulata-pachyderma* of *P. asplenioides* may bear much resemblance to the larger forms of *P. sharpii* — so much that the latter species may be overlooked in the field for the former. When the two occur together, the dull but brighter green *P. asplenioides* stands in contrast to the strongly shiny, olive-green or somewhat brownish *P. sharpii.* Both species produce fine marginal teeth, very numerous normally; both may have bulging trigones (but the mod. *pachyderma* is the only one so far found of *P. sharpii,* while such a modification is relatively rare in *P. asplenioides*); both may have brownish stems (rather rarely deep brown in *asplenioides,* but distinctly so in *Schuster* 25236, Dry Falls, N. C.). In spite of the habitual similarities, several major differences suggest the two species are only distantly related: (1) The oil-bodies of *P. sharpii* are homogeneous (segmented in *P. asplenioides*); (2) the cells of *P. sharpii* average less than 20 x 25 μ in the leaf-middle (25-32 μ in *P. asplenioides*); (3) the leaves of *P. sharpii* are strongly postically secund (more widely spreading in all but exceptional forms of *P. asplenioides*).

4. Confusion with *P. arctica:* Until the differences were pointed out by Persson (1946), *P. asplenioides* was confused with this species, as in Frye and Clark (1945). The two species, as emphasized by Persson, appear to differ chiefly in the smaller, less translucent cells of *P. asplenioides,* contrasted to the

more translucent, lighter, larger (36-45 μ) cells of *P. arctica*. The differences, as Persson points out, are probably correlated with polyploidy; see Table I. As is pointed out under *P. arctica,* there appears to be a further differentiating feature which has been insufficiently stressed: in *P. arctica* only the mod. *integrifolia* appears to be normally produced, and the plants are often more or less shiny when dry; in *P. asplenioides* there is variation from mod. *integrifolia* to mod. *dentata,* and the plants are usually nearly or quite dull when dry.

5. Confusion with *Plagiochila tridenticulata:* Douin (1924) suggested that the dubious "species" *P. stableri,* known from a single English Collection, represented a juvenile form of *P. asplenioides*. Müller (1942) has shown that *P. stableri* is identical with *P. tridenticulata*. As Müller points out, juvenile bilobed-leaved forms of *P. asplenioides* "go over" into forms with nearly entire leaves, *i.e.,* only the earliest leaves show the deep bilobing characteristic of *P. tridenticulata*. The invariable production of entire leaves soon after the development of a new shoot (whether by regeneration from a leaf, or growth from a spore) therefore will separate *P. asplenioides* from *tridenticulata*. Furthermore, *P. tridenticulata* differs in the position of the branches, which at first issue at virtual right angles from the parent shoot, soon become geniculate and continue nearly or quite parallel to the parent shoot (Fig. 21:6); such geniculate branches do not occur in *P. asplenioides*. In cases of doubt, perhaps the simplest separation is afforded by the oil-bodies, which are homogeneous in *P. tridenticulata,* segmented in *P. asplenioides;* also, the leaves of *P. tridenticulata* are caducous, those of *P. asplenioides* persistent.

6. Confusion with *P. satoi:* The Alaskan collections, referred by Evans to *P. asplenioides,* in part appear to represent "a form of *P. satoi*" (H. Inoue, in litt., Dec. 2, 1957). I have checked several Oceanic Alaskan plants, small in size, with subrotundate leaves bearing distinct marginal teeth. These appear to differ truly from the very closely allied *P. asplenioides* in the smaller size of both marginal and median leaf-cells. The very small submarginal cells (17-20 μ wide) and median cells (21-25, rarely to 27-28 μ wide) of *P. satoi* separate it from all forms of *P. asplenioides*. Other differences are discussed under *P. satoi* (p 156).

7. Confusion with *P. aspleniformis:* The subtropical *P. aspleniformis* is superficially almost identical with the laxer forms of *P. asplenioides*. However, *P. asplenioides* differs as follows: leafy propagula never produced; plants relatively dull and not strongly shiny when dry; plants never a peculiar pellucid yellowish green in color; branching exclusively intercalary. These differences at one time were considered so slight that *P. aspleniformis* was placed as merely a subspecies of *asplenioides*. However, careful comparison indicates that the many similarities between the two species are the result of parallel evolution and do not indicate any close relationship (see under *P. aspleniformis*).

8. Confusion with other genera: Inexperienced students may often misidentify species of *Solenostoma, Jamesoniella* and other Jungermanniaceae with the mod. *integrifolia* of *P. asplenioides*. The segmented oil-bodies, more or less discrete cnemis, and the small underleaves should prevent confusion with these genera.

The difficulty in determining extreme forms of *P. asplenioides* is well-illustrated by material of *Schuster* 18337 (Turkey Run State Park, Ind., pH 5.4, 5.8, 6.2; with *Scapania nemorosa, Diplophyllum apiculatum, Radula obconica* on shaded sandstone wall). These plants, largely very small (1.5 mm wide or less) fail to show, in most cases, the differentiation into basal rhizomatous stem and rhizoid-free leafy stems, the stems all being more or less freely rhizoidous and decumbent, as well as leafy. The leaves are quite atypical and somewhat juvenile (apparently due to the extremely unfavorable environmental

conditions): they are mostly sharply bilobed to slightly bilobed, occasional ones with supplementary small teeth. In their shape they closely approach those of *P. columbiana,* and those of *Pedinophyllum interruptum* var. *pyrenaicum.* However, the much smaller cells separate the material from *P. columbiana,* while the strongly collenchymatous cells, with bulging trigones in the median cells and thick-walled marginal cells, separate the plants from *Pedinophyllum.* Such juvenile plants have been the cause of confusion with the latter genus. In the present collections, the few well-developed shoots present are up to 2.2 mm wide and then show a few of the unlobed leaves, with several fine marginal teeth, characteristic of *P. asplenioides.*

Variation.—It has been indicated, in the section immediately preceding, that *P. asplenioides* shows an extraordinary amount of variation, having on this account been confused with a variety of other taxa. Although much of this variation is unquestionably adaptative, the work of Höfler has shown that a variety of physiologically distinct, hence genetically distinct, biotypes exist (Schuster, 1957). Furthermore, interpreted broadly (to include *P. ovalifolia, P. arctica,* and *P. major*), *P. asplenioides* s. lat. encompasses a series of populations that cannot, under any conditions, be interpreted as mere environmental modifications. Cell-size appears to be sufficient to separate *P. satoi* (p. 158). Cell-size alone, coupled with major differences in leaf form allow us to recognize, in addition, a series of more or less discrete phases that appear to be genetically distinct; these, for sake of orientation, may be ordered as follows:

1. Leaves entire or finely dentate (teeth 1-3, rarely 4 cells long x 1-2, rarely 3 cells wide at base); androecial bracts subentire or finely toothed; branches all intercalary; perianth-mouth entire or finely dentate, vertically truncate 2
   2. Cells small in leaf middle, averaging no more than 25-30 (33) μ wide. *P. asplenioides.* .... a
      a. Leaves entire or virtually so, typically reniform-rotundate, laterally appressed, dorsally secund and connivent. Arctic. .... *P. asplenioides* var. *subarctica*
      a. Leaves variable, toothed to entire, but typically ovate, and typically laterally patent to suberect, in lateral aspect often more or less postically secund, often conspicuously so. Non-arctic. ....*P. asplenioides* s. str.
   2. Cells of leaf middle large, averaging (28) 30-40 μ wide. 3
      3. Arctic in range; 2-4 (4.5) mm wide; cells usually larger, averaging most often 35-40 μ wide; leaf-margins entire or subentire, rarely with a few (5-15) scattered teeth. *P. arctica.* .... b
         b. Leaves variable, ovate or essentially so, usually laterally patent in antical aspect, sometimes suberect but not antically connivent and erect-appressed. .... *P. arctica* var. *intermedia*
         b. Leaves reniform or rotundate-reniform, erect appressed and usually antically connivent. .... *P. arctica*
      3. Oceanic and suboceanic in range; 4-6 (7) mm wide; cells usually smaller (28) 30-33 (35) μ in width in leaf middle; leaf-margins typically freely and closely dentate with 25-35 fine teeth. .... *P. major*
1. Leaves with the ability to produce rather variable and rather coarse teeth (the larger, near the apices of the leaves, often lobe-like and 5-6 [7-8] cells long x 3-5 cells wide at base), unable to produce entire-margined modifica-

tions; androecia with apices and postical margins of bracts closely and rather sharply toothed; with the ability (not always realized) to produce terminal branches. Perianth mouth obliquely truncate, often ± incised ventrally, very closely shortly ciliate-dentate). East Asia. ....*P. ovalifolia*

It could readily be postulated that all of the preceding taxa belong to a single, ancient, polymorphous species. The conspicuous tendencies which several of these taxa exhibit for parallel modes of modification can be interpreted both in favor of, and against, such a postulate. However, a very conservative treatment would result in total chaos, since *P. asplenioides,* restricted as narrowly as I have circumscribed it above, still remains a very polymorphic taxon. The following pages will attempt to delineate some of the more cardinal modifications *within* the species, as defined above.

Historical Survey.—The notoriously wide variability in *P. asplenioides* attracted attention at an early date and led to several attempts to "split off" the more marked but environmentally-induced extremes (*P. nodosa, P. porelloides, P. dillenii*) long before the putatively genetic segregates enumerated above were discovered. This variability was well known to the earliest workers with Hepaticae, and even during the period of polynomial nomenclature attempts were made to recognize two species. As Hooker (1816) points out, the *"Lichen Asplenii facie, pinnis confertioribus"* was separated as a distinct species from the *"Lichen Asplenii facie, pinnis laxioribus"* by Dillenius (Historica Muscorum, pp. 482, 483), although, as emphasized by Hooker, "only out of deference to preceding botanists." Even at this early date precedent existed for attempted division of the species into segregates! Hooker, with his customary acumen, stated that the little differences in the leaves, upon which these two "species" were based, "are to be found not only upon plants growing in the same patch, but are even to be met with on the same individual . . ."

Not only were there early attempts at a division of this species into segregate species, but the unending amount of variation of this ubiquitous species stimulated attempts, even during early times, to divide the species into many primary forms (varieties) and secondary forms (formas). The first, and to date most thorough, of these attempts was that by Nees (1833) whose classification was reviewed by Schiffner (1908) and Müller (1910). Since the putative genetic basis for the primary and secondary forms can only be demonstrated by extensive experiments, which are to date lacking, it is in the writer's opinion pointless to attempt to deal with most of these variants on a taxonomic basis. It must, however, be stressed that at least some data is at hand to show that the exceedingly robust populations of *P. asplenioides* differ physiologically, hence genetically, from the smaller forms. Since, presumably, this species will show a wide amount of minor genetic segregation, recognition of only two forms would result in an entirely over-simplified and untrue picture of the variation of the species. The vast majority of varieties and forms described within the species will, in the opinion of the writer, prove non-genetic, or, conceivably, are

the result of single gene differences and therefore deserve no nomenclatorial distinction. Until much more is known about genetic *vs.* nongenetic variation in *P. asplenioides,* it therefore seems incumbent on us to disallow most of the nomenclatorial entities with which the literature is replete.

Müller (1910) presumes that the various "forms" of *P. asplenioides* are all environmentally induced, and fall into four basic types: (1) The mesic form of woods, var. *typica;* (2) the very robust form of moist shaded place, the plants to 10-15 cm tall, var. *major;* (3) the small forms, growing mostly in compact patches, of xerophytic sites; vars. *minor, devexa, porelloides, humilis;* (4) the lax form of mountain streams, hydrophytic; var. *riparia.*

This represents an oversimplification, *P. asplenioides* consisting of several ecotypes (and possibly even of ecospecies), as well as of ordinary environmental modifications. Neither the attempt to resolve the numerous evident variants of the species as in Müller, nor the attempts by Schiffner (and largely following him, Macvicar) make any real attempt to distinguish between environmental and genetic variants. The latter authors distinguish seven "varieties," some of which include a series of "formas." The following key attempts to separate these, as well as two putatively genetically distinct varieties.

a. Leaves distinctly, often strongly dentate. .... b

b. Plants robust, 4-7 cm tall and 3-4 mm wide, or more. c

c. Leaves spreading laterally, little secund, little imbricate; mesic forms; pale green or olive-green; mostly 5-10 cm tall. .... d

d. Plants very robust, 8-10 cm tall x 5-6 mm wide; plant pellucid and pale green; slightly branched. ....var. *major Nees*

d. Plants less robust, 4-7 cm tall x 3-4 mm wide; usually deep green, richly branched. ....var. *typica* (= *confertior*)

c. Leaves strongly postically secund, deltoid-orbicular and very broad, closely imbricate, the whole antical margin strongly reflexed; posterior margins strongly dilated and projecting backward to form a crest with that of the opposed leaves, very closely ciliate-dentate; plants to 3.5-5 cm tall, erect, pale olive-yellow ....var. *devexa* Carr.

b. Plants small, 2-3 cm long, in dense, usually deep green tufts, leaves imbricate, strongly convex (the lower leaves often entire or subentire); very similar to var. *typica,* but smaller. ....
..........Var. *minor* Lindenb. (= *P. dillenii* Tayl.)

a. Leaves entire or virtually so (except, occasionally, near ♀ bracts). .... e

e. Plants robust, 5-10 cm tall x 3.8-6 mm wide .... f

f. Plants tall, erect, in pale green tufts; leaves large and imbricate; 8-10 cm tall x 5-6 mm wide (like var. *major,* but leaves essentially entire).
..........var. *major* fo. *subintegerrima* Schiffn.

f. Plants less robust, lax; leaves usually distant to approximate, narrower; 5-9 cm tall x 3.8-5 mm wide. ....var. *riparia* Breidl.

e. Plants small and impoverished, 1-3 cm tall x 2-4 mm wide. .... g

g. Leaves ovate to subrotundate, laterally ± patent, convex. .... h

h. Leaves on mature plants (3.5-4 mm wide) retuse to shallowly, asymmetrically bilobed, occasionally with a few accessory teeth (Fig. 9:9); plants without stolons, loosely prostrate; perianth very broad at mouth, campanulate. ....var. *obcampanulata* var. n.

h. Leaves rounded at the apex, except in juvenile plants; perianth parallel-sided or nearly so except at base. i
i. Like var. *minor,* but entire-leaved or virtually so; stolons absent or rare; plants 2-3 cm long, prostrate or ascending. ....var. *minor* fo. *porelloides* (Torr.) Schiffn. (or var. *porelloides* (Torr.) Schiffn.)
i. Very small, 1-2 cm high, often suberect or erect, with numerous stolons; leaves imbricate, convex; yellow-green ....var. *humilis* Lindenb. (questionably identical with var. *humilis* of Nees)
g. Leaves reniform to rotundate-reniform, much broader than long, erect to erect-appressed and antically secund, not convex; with numerous stolons; leaves closely imbricate, yellow-green (Fig. 10A) ....var. *subarctica* Joerg.

The above classification could well be simplified, by attempting to separate out putatively genetic variants from minor genotypes and environmental modifications, limiting the term variety to the former, and tentatively using the term forma for the latter, as follows:

1. Plants very robust, usually 8-10 cm tall x 5-6 (7) mm wide; cells larger and more pellucid, (30) 33-35 μ wide. ....var. *major* Nees = *P. major* (Nees) S. Arnell a
a. Leaves copiously dentate. ....var. *major* Nees, typical
a. Leaves entire or virtually so. ....fo. *subintegerrima* Schiffn.
1. Plants much less robust, usually (1.5) 2-7 cm tall x (1.5) 2-5 mm wide; cells opaque, smaller (averaging 25-28 [30] μ wide). .... b
b. Leaves very variable in shape, but basically ovate, averaging clearly longer than wide (or rarely, in small forms, as wide as long), $\pm$ strongly adaxially convex, never erect-appressed; stolons absent or usually few. var. *asplenioides.* c
c. Leaves freely and rather closely dentate. .... d
d. Leaves laterally patent, little secund, little imbricate (Fig. 8: 4-5); mostly 5-7 cm tall (or, "var. *minor*" only 2-3 cm tall); with the leaves with postical bases not opposed to form crests. ....fo. *typica* (including var. *minor*)
d. Leaves strongly postically secund, deltoid-orbicular, broad, imbricate, the postical margins dilated and reflexed to form crests with the opposed leaf bases (Fig. 8: 1); 3-5 cm tall. ....fo. *devexa*
c. Leaves entire or subentire, occasionally shallowly and asymmetrically bilobed at the apex. .... e
e. Mature plants with entire-margined leaves, not bilobed at apex (Fig. 8: 2); perianth narrow at mouth, not campanulate in outline, the mouth never reflexed. .... f
f. Plants very robust, lax, 5-7 (9) cm tall x 3.8-5 mm wide; leaves laterally patent. ....fo. *riparia* Breidl.
f. Plants small, 1-3 (4-5) cm tall x 2-4 mm wide .... g
g. Prostrate, like fo. *typica,* but entire-margined or virtually so; stolons absent or rare; plants 2-3 (4-5) cm tall, with little imbricate leaves (Fig. 13:1). ....fo. *porelloides* (Torr.) Schiffn.
g. Ascending or erect, often caespitose, only 1-2 cm high, with numerous stolons; leaves imbricate, yellow-green. ....fo. *humilis* (Lindenb.)
e. Mature plants with retuse to asymmetrically and shallowly bilobed leaves, with occasionally a few small accessory teeth (Fig. 9: 9); habitually like *P. columbiana,* but small-celled; perianth obcampan-

ulate in lateral profile, broad and often reflexed at mouth; plant lax-leaved to loosely imbricate-leaved, in wet sheltered sites, but with strong development of trigones (Fig. 9: 10). ....var. *obcampanulata* var. n.

b. Leaves broadly rotundate to reniform, at least 1.2-1.5 × as broad as long, nearly flat, erect-appressed and somewhat antically secund; stolons abundant; plant small, 1-2 cm high, yellow-green, erect and caespitose. High arctic. (Fig. 10A) ....var. *subarctica* Joerg.

The last two taxa proposed are described in detail on subsequent pages (pp. 138-139). Further description of the other variants listed above seems unnecessary, except to add that the var. *major* deserves probably a higher status (see p. 143).

Utilizing the divisions outlined previously, the modifications and variations in the various individual organs may be outlined as follows:

Stem.—Although our other species of the genus almost always show a distinct differentiation into rhizogenous primary stems, with reduced leaves, and aerial leafy stems, *P. asplenioides* when growing under environmentally "difficult" conditions often totally lacks any such differentiation, possessing only ascending to decumbent, rhizoid-producing, leafy shoots and a few to abundant stolons (var. *humilis* Lindenb., and extreme derivations of it). Such forms furthermore, correlated with poor nutrition, retain a more or less juvenile form and therefore possess more or less entire, dorsally relatively short-decurrent leaves. These plants, especially when growing on moist sites, may show a poor differentiation of the medulla, and then lead easily to confusion with *Pedinophyllum* (see p. 61).

In shade forms, and particularly in plants from moist sites, the axis is commonly green or barely brownish-tinged; the cortical cells may then be only slightly thick-walled. Inversely, robust sun forms often have wiry, firm stems that are a clear reddish-brown in color; associated with this the cortical cells in 2-5 layers may be exceedingly thick-walled and almost bast-fiber-like.

Although *P. asplenioides* when well-developed has a stem 13-16 cells in height with a brownish or yellowish-pigmented cortical region of thick-walled cells some 2-3 cell-layers thick, we find (associated with differences in moisture and nutrition) much variation in stem anatomy. In *Schuster* 25236 (a mod. *pachyderma,* Dry Falls, N.C. = var. *obcampanulata*), the stem of the larger plants is only 11-12 cells high, with the 2-3 stratose cortex well-differentiated (Fig. 9:8). More or less juvenile stems and ascending leafy shoots may show a stem no greater in height, with virtually no differentiation of the cortex; the latter consists of cells in one layer that are somewhat smaller than the medullary cells (in cross-section), with the walls somewhat more thickened than those of the thin-walled medullary cells. Such forms, usually entire-leaved, closely approach *Pedinophyllum* in stem anatomy. The aerial stems, at least, of *P. asplenioides* are never mycorrhizal (the leafy stems of *Pedinophyllum* usually have the ventral 2-3 cell-layers mycorrhizal; Fig. 6:1).

The slightest degree of cortical differentiation, in *P. asplenioides,* occurs in small, high arctic extremes with reniform leaves (var. *subarctica*). In these the stem is only 10-12 cells high, and the cortex consists essentially of an unistratose layer (Fig. 10A:7). In such cases we find a very close aproximation to the stem anatomy of *Pedinophyllum,* although the cortical cells are still differentiated in being somewhat smaller in diameter, and somewhat tangentially flattened, as compared to the more leptodermous medullary cells.

The degree of differentiation of the cortical cells, as seen in surface view, is also exceedingly variable. In robust, well-developed plants the cortical cells are moderately elongate, often 3.5-4.5 × as long as wide, brownish, and very thick-walled. Inversely, in the small plants of var. *subarctica* the cortical cells are only (1) 1.5-2 (2.5) × as long as wide, irregularly short-rectangulate, only slightly thick-walled, and virtually colorless.

Leaves and Leaf-orientation.—Much of the variation in *P. asplenioides* is in the form of the leaves and of the leaf-cells (Figs. 8; 9:3-4, 6-7; 10A:1-3; 13:4-5). Under a wide variety of suboptimal conditions, the leaves are subentire, except for occasional emargination of the apex; then the plants possess a juvenile facies that often makes them unrecognizable except to the experienced eye.

However, the "variety" *major* Nees, which attains a height of 8-15 cm and width of 5-6 mm or more, produces a subentire modification (fo. *subintegerrima* Schiffn.). This "variety" appears capable of producing its own series of modifications, parallel to those of more typical *asplenioides,* suggesting that perhaps it is a distinct species, *Plagiochila major* (Nees) S. Arnell. Macvicar (1926, p. 225) also states that "it has generally been acknowledged that [the varieties and forms of *P. asplenioides*] pass into one another, but I am not at all convinced that this is the case with the var. *major.* At least, it is much more the distinct form, and seldom gives rise to any difficulty in distinguishing it." Supplementary evidence for this is available from distribution (p. 143). *P. major,* as far as I can ascertain, is lacking in eastern North America. Consequently, *P. major* must be a genotypically discrete form, since it is unthinkable that only Europe possesses the special microenvironments which would induce its development (if it were a modification). The report of var. *major* from Maine by Parlin (1939) is untrustworthy.

Under other conditions, the leaves are broadly elliptical in shape, rather than ovate, and widest near their middle; this may be combined with the juvenile entire marginal condition (Fig. 13:4), or with development of the marginal dentition (Fig. 9:4). The leaves of small innovations, or regenerations, are normally bidentate (see Douin, 1924; Müller, 1942). On otherwise normal-appearing plants of large size, this shallow bilobing of some or all leaves may be clearly apparent (Fig. 9:9), and the plants then acquire a facies similar to that of *P. columbiana* (Fig. 14), as well as to that of *Pedinophyllum interruptum* var. *pyrenaicum.* Such plants represent the var. *obcampanulata.*

The cnemis, or dorsal fold, though normally well-developed in this species (Fig. 8) is often vestigial in plants with juvenile, more or less entire-margined leaves, and the characteristic plagiochiloid facies is

then, of course, scarcely apparent. The dorsal fold is commonly quite absent in the var. *subarctica* (Fig. 10A). Only rarely is the cnemis so poorly developed that confusion with *Pedinophyllum* can conceivably occur.

Not only is the leaf-form rather polymorphic in *P. asplenioides*, but so is the leaf-orientation. In the hygromorphic forms (mod. *angustifolia-integrifolia-leptoderma-laxifolia* = var. *riparia*) the leaves spread laterally; from this extreme there occurs variation to an xeromorphic extreme (mod. *latifolia-denticulata-meso-vel-pachyderma-densifolia*) in which the leaves are nearly suberect and (in lateral view) are clearly postically secund, much as in *P. sharpii* and *alaskana;* this extreme, with postically secund leaves, is sometimes called the var. *devexa* Carr. (Fig. 8:1). In extreme forms (var. *subarctica*) the leaves attain the opposite orientation; they are antically secund, become appressed to the stem (Fig. 10A:5), with the consequence that a facies like that of *Nardia compressa* is simulated!

Not only is there a bewildering range of variations in leaf shape and orientation, but *P. asplenioides* shows a wide range of variability in merophyte length. In some instances the leaves are distant to barely contiguous; in others they may become quite closely imbricate. Such wide variation in merophyte length is a primitive feature, the more specialized species of the genus being usually much more rigid in this respect.

Dentition.—It has already been demonstrated that variation occurs from entire-margined to distinctly dentate phases. To some extent the capability to develop teeth must be genetic in nature. However, culture experiments have shown that the species will show variation from entire-leaved to dentate-leaved extremes, depending on environmental conditions. Such variation can occasionally be observed in "wild" plants, as Hooker (1816) long ago noted.

Some of the closely allied taxa "behave" somewhat differently in regard to dentition. For example, *P. ovalifolia* is typically more coarsely dentate (p. 126) and appears unable to produce entire-leaved extremes on mature shoots. Inversely, *P. arctica* s. str. appears unable to develop phases with the copious, if fine, dentition of *P. asplenioides*, although the leaves occasionally develop scattered marginal denticulations (Figs. 10B, 11). Within *P. asplenioides* s. str. there are wide variations in the degree to which the teeth are elaborated, and in the extent to which the teeth extend down the antical leaf-margins.

The mod. *dentata* may have the teeth absent along the antical margin, except in the distal one-fourth (Fig. 9:3, 6), or they may be present (at least on isolated leaves) to within 0.2-0.3 of the base (Fig. 9:4), although they are smaller and less conspicuous along the antical margin, usually quite oblique, and usually not discernible unless the leaf is flattened. Such teeth occur, *i.e.*, in the closely allied *P. satoi*, in *Frye* 230 (Alaska) and in typical *P. asplenioides*, as in *Schuster* 24725 and 39372 (North Carolina), hence are not restricted to populations from one region, nor are limited to *P. asplenioides*.

The teeth of the leaves are very variable: when well-developed, they are in part spinous and up to 3-5 cells long x 2-3 cells wide at base, their apices often being formed of 2, rarely 3 superimposed cells. The terminal cells, on weak teeth, are often little longer than wide (Fig. 9:1); on the phases with strongly marked teeth the terminal cells may be slender and narrow, drawn out to a sharp point, and may range from 11-12 x 35 μ up to 13-14 x 40-42 μ—in other words, average 3-3.5 $\times$ as long as wide. Such sharply differentiated terminal cells are more commonly present in the related *P. ovalifolia*, although, as is evident, certainly not confined to it. None of the apical teeth are normally elaborated as incipient lobes in any form of *P. asplenioides*. On weaker plants, with the dentition less marked, the teeth may be only 1-2 cells long, with little differentiated terminal cells only 1.2-1.5 (2) $\times$ as long as wide.

Leaf-cells.—The leaf-cells vary to some degree in size (Table I). *P. asplenioides* almost always occurs as a mesic or hygric type, with small trigones (mod. *leptoderma*); relatively rarely we find, even under very moist conditions, a mod. *mesoderma* or *pachyderma*, with bulging trigones (Fig. 9:10). The fact that there are forms of *P. asplenioides* from exceedingly moist, shaded humid sites (as *Schuster* 25236, Dry Falls, Highland, N.C., from wet ledges near a waterfall, in shade), which possess bulging trigones suggests that there are different races of the species, differing in the stimulus necessary for trigone production. As is further suggested below, there is correlated with such trigone production the development of papillose oil-bodies of a different type from those usual for the species, suggesting definitely that a discrete race (or possibly distinct ecotype) is at hand; this is described on p. 139 as var. *obcampanulata*. In almost all forms the marginal 1-2 rows of cells tend to be somewhat equally thick-walled (Fig. 9:1). The degree of development of such a border is quite variable; it may be lacking (Fig. 12:3). For instance, the mod. *mesoderma-denticulata* (*Schuster* 25007, Whitewater Gorge, N. C.) portrayed (Fig. 8:1-4) shows concave trigones of intramarginal cells correlated with a well-developed border of thick-walled marginal cells, the cells hardly collenchymatous in the marginal rows (Fig. 9:1).

P. asplenioides normally has coarsely segmented oil-bodies, occurring 4-8 cell (*Schuster* 18337, Turkey Run Park, Ind.; *Schuster* 25007, Whitewater Gorge, N.C., Fig. 9:2).

This is also the case in a leptodermous form (4-5 cm long x 4 mm wide) which corresponds nearly to var. *typica*, but has very broadly orbicular leaves as wide or wider than long, sparsely dentate. This has 3-7 very coarsely segmented oil-bodies per cell. This plant (from Scotland: Callander, Pertshire, leg. *E. W. Jones*) has the larger oil-bodies 4-5 x 9-10 μ or 6 x 9-12 μ, formed (in surface view) of 8-12, rarely 15 coarse, protruding segments 2-3 μ in size; the smaller oil-bodies (3 x 5 to 4 x 6 μ) are only 4-6 segmented.

Exceptionally, only 2-3 oil-bodies may be found in smaller cells. However the more or less pachydermous form (*Schuster* 25236, Dry Falls, N.C. = var. *obcampanulata*) has oil-bodies occurring 5-12 per

cell, with the individual oil-body appearing superficially nearly homogeneous (Fig. 9:10), but actually formed of many small (less than 0.8 μ), slightly protruding oil-globules (therefore appearing somewhat papillose, rather than segmented).

The above statements on cell and oil-body form are based on study of the smaller forms of the species (1-7 cm tall). The very robust "variety" *major*, as is stated above, possibly should be called a discrete species, *P. major* (Nees), not only because of the more robust size, but also because of the tendency to possess larger leaf-cells. I have seen only a little material of *major*, but this shows consistently somewhat larger leaf-cells than typical *asplenioides*. In this *P. major* approaches *P. columbiana* and *P. arctica*. English material (Borrowdale, Cumberland, 19 May, 1945, *D. Banwell*), of *P. major* fo. *subintegerrima*, for instance, shows median leaf cells that average 33-35 μ wide. By contrast, more typical *P. asplenioides*, also from England (Callander, Pertshire, Scotland, July 30, 1953, *E. W. Jones*), shows median cells averaging 26-30 μ wide. The problem of whether to recognize *P. major* as a distinct species, and its relationships to *P. asplenioides* and *P. arctica* are subsequently discussed (p. 144). This problem is complicated to a great extent by the obvious tendency of *P. asplenioides* to develop larger leaf-cells as one goes from the eastern portion of North America to the northwest (see Table I).

The preceding statements as to variability in cell size, between *P. asplenioides*, on one hand, and *P. major* and *arctica*, on the other, are applicable to all of our plants *except* for the series of populations sampled from British Columbia and Alaska. In the Alaskan plants we find a distressing amplitude of variation in cell size. Aside from all other criteria for separating these taxa, cell size and size of plant allow us to divide the collections seen into *three* categories: (*a*) robust plants, almost always with very broad leaves that are antically secund, with very large pellucid cells, averaging 34-40 μ wide in the leaf-middle; these plants represent luxuriant phases of true *P. arctica;* (*b*) superficially identical plants, also very robust, with leaves often ovate, sometimes broadly rotundate, the leaves sometimes antically connivent but often laterally more or less patent, with medium-sized cells ([28] 30-35 μ wide in the leaf-middle); these plants, when patent-leaved, might be interpreted as a mod. *integrifolia-parvifolia* of *P. major;* (*c*) much smaller plants, in which the median cells fail to average over 25-27 μ wide. The plants of type *a* are readily referred to *P. arctica*. The plants of type *b* represent a considerable problem as regards their disposition. This is not made easier by the fact that sometimes isolated leaves with "normally" small cells bear sharply defined areas with very large cells, whose size perfectly match those of *P. arctica*. The plants of type *b* bear somewhat larger leaf-cells, in most cases, than "normal" *P. asplenioides*. They may represent, at least in part, *P. major*. Finally, the plants of type *c* are a problem: they have cells that are definitely smaller than in "normal" *P. asplenioides*. These plants appear to represent the Japanese *P. satoi* (see p. 158). Indeed, the study of the *P. asplenioides* complex is greatly complicated when the Alaskan populations are studied, since very few of these appear to be referrable to *P. asplenioides* s. str. Orthodox taxonomic approaches in the complex, therefore, appear to possess only limited utility and validity.

The preceding essay has indicated that much of the variability exhibited by *P. asplenioides* is either "somatic," *i.e.*, environmentally induced, or is possibly the consequence of expression of single gene differences. However, at least two of the variations recently placed

under *P. asplenioides* appear to deserve formal recognition: *P. asplenioides* var. *major* as a distinct species (p. 143) and the var. *sub. arctica* as a distinct race (or perhaps subspecies) of *P. asplenioides.* In addition, a further variety of putative genetic origin is described, as var. *obcampanulata.* The two latter varieties are described on succeeding pages.

PLAGIOCHILA ASPLENIOIDES var. SUBARCTICA Joerg.
Fig. 10A

Plagiochila asplenioides var. *subarctica Joergensen,* Norg. Leverm. 173, 1934; S. Arnell, Ills. Moss Fl. Fennosc. I: 162, 1956.

Plant yellow-green, dull, *strongly laterally compressed, erect and caespitose,* 10-15 (20) mm high x 1.0-1.75 mm wide (lateral measurement). Stems *ca.* 200-250μ in diameter, the *cortex ill-defined, unistratose or locally 2-stratose,* formed of only moderately thick-walled, cells 18-21 μ wide x 28-32 μ long on an average; medulla of leptodermous cells 20-30 μ in diameter; branching exclusively intercalary, with both leafy branches, and *negatively phototropic stolons,* originating in ventral halves of leaf axils. *Leaves broadly orbicular to reniform,* from a minimum of 1350 μ wide x 900 μ long to 1600 μ wide × 1260 μ long up to 1830-1900 μ wide x 1200-1220 μ long (*width 1.25-1.6 the length*), *erect to erect-appressed and somewhat antically connivent, the shoots appearing strongly laterally compressed; leaf margins entire,* the dorsal base longer decurrent than postical, but relatively short-decurrent; *dorsal margin not or hardly reflexed,* the apex erect or only occasionally somewhat reflexed. Cells as in typical *P. asplenioides*: rather thin-walled and with small to weakly bulging trigones, the *marginal averaging* (*16*) *17-20* μ, quadrate; *median 23-25 x 23-28* (*30*) μ; basal 23-28 (30) x 25-38 μ; oil-bodies (2-4) 5-8 (9) per median cell, coarsely segmented, from 4 x 6-7.5 μ to 4.5-6 x 10 μ. Underleaves obsolete. Wholly sterile.

Type.—Norway (Dovre and Nordland).

Distribution.—Reported only from Norway, this plant occurs in typical manifestations in northern Alaska and northern Ellesmere Island.

ELLESMERE ISLAND: Shore of Arctic Sea, edge of Polar Ice Pack, just west of Cape Belknap, *ca.* 1.5 mi. from Alert, NE. Ellesmere Island, 82°32′ N. (*Schuster* 35625, 35750). ALASKA: Umiat and vicinity (*Steere* 17108!; a mod. *parvifolia,* with the leaves only 1100-1125 μ wide x 750-875 μ long); Driftwood Camp, near headwaters of Utukok R., N. slope of De Long Mts., Brooks Range, *ca.* 68°53′ N., 161°10′ W. (*Steere* 16602!; leaves cordate at postical base, rounded, very broad, entire-margined). [Two other Alaskan collections represent transitions to var. *subarctica*: Southwest end of Chandler Lake, Endicott Mts., Brooks Range, *ca.* 68°12′ N., 152°47′ W., 3000 ft. (*Steere* 18244; cells only 24-27 μ wide in leaf-middle); area between Mt. Araga and Smith Lakes, just W. of Etivluk R., Endicott Mts., Brooks Range, *ca.* 68°43′ N., 156°30′ W., 2000 ft. (*Steere* 17859!; cells 25-33 μ wide in leaf-middle).] QUEBEC: Grand Ile, Archipel de Mingan (*Marie-Victorin & Rolland-Germain*

49592, *p. p.*, among *Scapania cuspiduligera, Blepharostoma trichophyllum, Distichuim capillaceum, Mnium ornithorhynchum, Amblystegiella sprucei, Myurella julacea*).

This variant occurs in damp, calcareous high arctic tundra, on northern Ellesmere Island, associated with *Lophozia pellucida* Schuster, *Arnellia fennica, Lophozia quadriloba* and *L. heterocolpa harpanthoides, Blepharostoma trichophyllum brevirete* and *Scapania gymnostomophila;* also with such typical arctic angiosperms as *Saxifraga caespitosa, Papaver radicatum,* and *Salix arctica.*

It appears impossible to reconcile the anomalous features of this plant with mere environmental modification. The much broader than long leaves, characteristically almost reniform in shape, do not again occur in any of our species, except in the closely allied *P. arctica* which occurs in the same immediate region. It agrees with the latter in all respects save in the much smaller cells of the leaves, the fewer oil-bodies per cell, the smaller and narrower cortical cells of the stem, and the absence of teeth of the leaves. The latter feature, in the variable *P. asplenioides* complex, is probably meaningless; the former features suggest a difference in chromosome number. The cell size, in this variant, appears to range somewhat below that of typical *P. asplenioides* (see Table I).

It is of considerable interest, and surely significant, that in a few isolated leaves of this plant, there occurred sporadic regions with large cells (Fig. 10A: 8), similar in size to those of *P. arctica.* Evidently, as is the case with several other arctic hepatics, mosaic polyploidy occurs frequently, due possibly to sporadic polyploidy within the embryonic leaf.

It is possible that this plant, and the very similar *P. arctica,* should be united as races of a single high arctic species.

The closest relative among the various phases of *P. asplenioides,* to which varietal rank has been assigned, is the var. *humilis* Lindenb. It agrees with the latter in the often erect growth, yellow-green color, small size, essentially entire, imbricate leaves, and in the free production of stolons. It departs widely from the var. *humilis* in the nearly flat, rather than convex, and broad, reniform, rather than oval leaves.

Plagiochila asplenioides var. **obcampanulata** var. n.

Fig. 9:8-10

Plantae mediocres, pallido-viridis; folia patentia, ovata, integris vel plus minus bidentatis vel bilobatis; lobis parvis, obtusis vel acutis, marginibus integris; perianthii os 4-5 lobulatis. Typus: Dry Falls, Cullasaja R., North Carolina (*Schuster, Anderson, Jones* 29375).

Plants medium-sized, 3.5-4 mm wide x 3-5 cm long, light green, with stems somewhat brownish or olive, with aspect of var. *porelloides.* Leaves on some shoots partly entire and ovate-triangular, with narrowed but rounded apices, but in part *bidentate to slightly and asymmetrically bilobed at apex,* occasionally with a few small, irregular teeth, up to 1450 μ wide x 1800 μ long to 1500 μ wide x 1650 μ long,

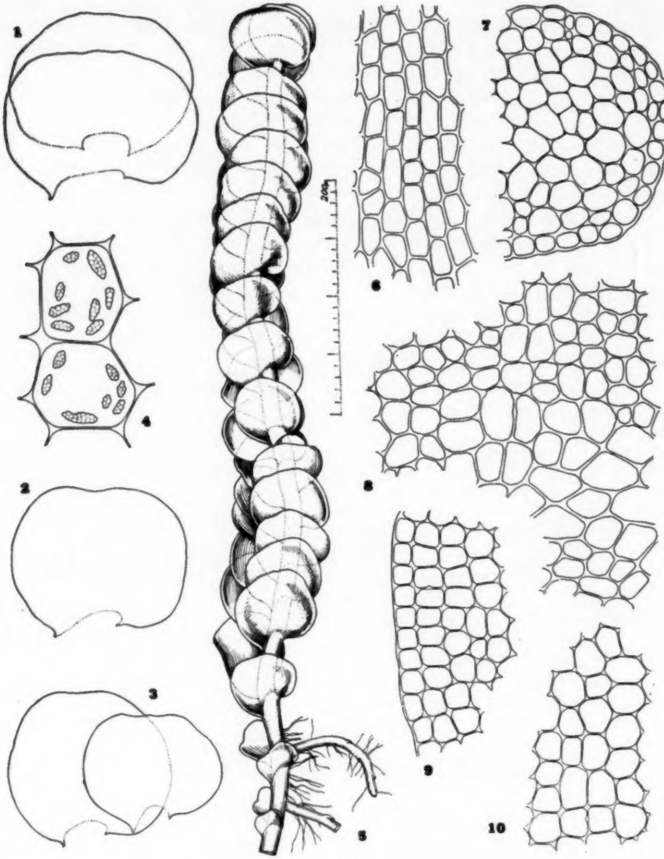

Fig. 10A.—*Plagiochila asplenioides* var. *subarctica* Joerg. 1-3. Leaves showing variation in shape, that in figs. 1-2 typical (x 14); 4. Two median cells, showing the typical number of oil-bodies (x 455); 5. Lateral aspect of mature shoot (x 12); 6. Dorsal cortical stem cells (x 172); 7. Stem cross-section (x 172); 8. Cells of apical half of leaf, showing both "normal" (smaller) cells and atypical, larger area of cells, possibly the result of polyploidy (x 172); 9. Apical cells (x 172); 10. Median cells (x 172). (All from *Schuster* 35625; north coast of Ellesmere Island at Alert; all figures drawn to same scale as corresponding figures in Fig. 10B; figures 6-10 drawn to the scale left of fig. 6).

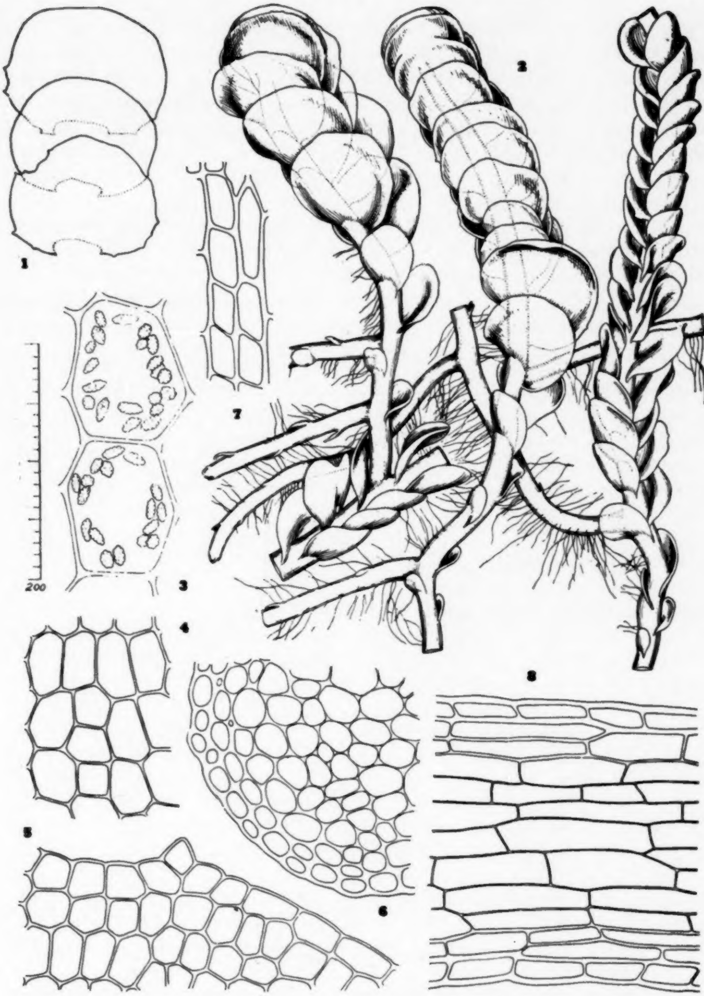

Fig. 10B.—*Plagiochila arctica* Bryhn. 1. Three leaves (x 14); 2. Three plants, the one at right possibly an old male shoot (x 17.5); 3. Two median cells (x 455); 4. Median cells (x 172); 5. Apical cells (x 172); 6. Stem cross-section (x 172); 7. Dorsal cortical stem cells (x 172); 8. Longitudinal section through center of stem (x 172). (All from *Schuster* 35191, "The Dean," south of Alert, Ellesmere Island; all figures drawn to same scale as corresponding ones of *P. asplenioides subarctica* in Fig. 10A; figs. 4-8 all to one scale, to left of fig. 3).

laterally patent, somewhat convex, *not at all postically secund,* only moderately decurrent antically, occasionally polymorphous and variably dentate. Cells of leaf-middle averaging 24-33 μ, with thin walls and prominent, *more or less bulging trigones,* even in the marginal cells (which are not at all thick-walled); oil-bodies ellipsoidal to baciliform to ovoid, 3.5-4 x 6-7.5 μ to 4-4.5 x 7.5-9 (11) μ, of rather small spherules (less than 0.8 μ diam.) thus *appearing finely papillose-segmented;* chloroplasts *ca.* 3-3.5 μ.

Perianths *relatively short, obcampanulate* in profile, broadened from base to apex, the wide, truncate *apex usually 4-5-lobulate,* the irregular and usually shallow lobes irregularly ciliate-dentate.

Type.—Schuster, Anderson, Jones 29375 (Dry Falls, Cullasaja R., near Highlands, Macon Co., N. C.).

This variant quite possibly represents a deviant form of the "var. *porelloides,*" but for the time being is considered a discrete variety of *P. asplenioides.* The variety differs from typical forms of the polymorphic *P. asplenioides* as follows: (1) mature shoots, even the perianth-bearing, with the dentition confined to two lobe-like apical teeth, with occasional, sparse, irregular, supplementary teeth sometimes present, or with the dentition quite suppressed; (2) cells with bulging trigones of interior and marginal cells — with no tendency towards production of marginal thick-walled cells; (3) oil-bodies formed of numerous minute, scarcely protuberant globules, appearing papillose rather than segmented; the oil-bodies numerous and usually 6-12 per median cell; (4) perianth obcampanulate in outline, becoming nearly evenly broadened from the narrow base to the broadly truncate apex, which may be lobulate and irregularly ciliate-dentate.

In addition to these differences, the variant has an unusual facies, the result of laterally flatly spreading leaves (on mature sterile shoots); the nature of the dentition of the leaves suggests juvenile phases of *P. asplenioides,* as well as *P. columbiana.* In fact, the plants of this variant appear midway between the two species, as regards gross appearance and cell-size. The leaves, although polymorphic in form, are much narrower than in robust *P. columbiana,* and often are ovate and quite entire (as in *P. asplenioides*). The cells average *ca.* 25-28 μ wide in the leaf-middle, and thus agree closely with those of *P. asplenioides* in size. However, the irregularly few-dentate leaves (of even the perianth-bearing shoots) are quite unlike any mature *P. asplenioides* the writer has seen.

Most distinctive are the perianths, which are gradually broadened to the very wide and truncate mouth, with the dorsal and ventral keels divergent from base to apex. In my experience, typical *P. asplenioides* never possesses such perianths, but rather shows parallel-sided perianths, at least twice as long as the truncate mouth is wide.

PLAGIOCHILA MAJOR (Nees) S. Arnell

Plagiochila asplenioides var. *major* Nees, Naturg. Eur. Leberm. 1:161, 1833.
Plagiochila major S. Arnell, Ills. Moss. Fl. Fennosc. I:162, 1956.

Plants *very robust, superficially similar to P. asplenioides,* often forming large mats, the aerial shoots subsimple or sparingly monopodially branched with ascending leafy intercalary branches whose basal leaves are much smaller; with rare intercalary branches from *below* postical leaf base; with occasional positively geotropic stolons from near the bases of the intercalary aerial branches. Shoots *often robust* (3.5) 4-6 (8) mm wide x (3-5) 7-10 (13) cm long, *slightly nitid when dry,* olive-green to light yellowish-green, occasionally slightly warm-brownish tinged when dry; stems often brown and rigid. Leaves typically *asymmetrically ovate* and 1.2-1.4 (1.5) × *as long as wide,* usually obliquely spreading in antical aspect, but laterally viewed clearly *postically secund* (in pale green hygrophytic phases sometimes subentire and laterally patent), the regularly arched postical margin and evenly rounded apex *with usually* 25-32 (35) *regular and slightly unequal, fine teeth* (from 1-2 cells high and 1 cell wide at base to 4-5 cells high x 2-3 cells wide at base), the nearly straight, strongly reflexed and often involute antical margin entire or subentire except near apex. *Cells very large and relatively pellucid,* the median averaging (28-30) 33-35 (37) μ wide x (35) 38-45 μ long, usually with thin or hardly thickened walls but with discrete to moderately bulging, sharply defined trigones; the marginal cells often slightly thick-walled; walls colorless or sometimes (in yellow-brown tinged sun forms) slightly yellowish. Underleaves vestigial, of a few minute cilia barely connate at base, ending in slime papillae. No asexual reproduction.

Dioecious. Female shoots in drying somewhat circinate, like sterile shoots, with the leaves imbricate, obliquely spreading to suberect in antical aspect, but in lateral aspect clearly postically deflexed and secund; bracts and subfloral leaves similar, broadly and asymmetrically ovate, the antical margin strongly reflexed-convolute for nearly its entire length, entire-margined basally, above base with a few oblique teeth; the rounded apex and virtually entire postical margins with regular, slightly unequal spinose-dentate, rather small teeth (of 1-2 superimposed cells, or 2-3 cells wide at base x 2-3, occasionally 4-5 cells high), the teeth averaging up to 28-35 along postical margin and apex, with 4-8 teeth of the antical margin that average appreciably smaller in size. Perianths narrowly obcuneate in lateral profile, up to 2.5 × as long as wide at the subtruncate mouth; the antical and postical keels not winged; the mouth only slightly oblique, laterally deflexed, with close but not approximate dentition similar to that of postical leaf-margins. *Spores ca.* 12 μ; *elaters* 6 μ *in diameter* (teste Arnell, 1956).

Type.—Western Europe.

Distribution.—Apparently more oceanic and much more limited in distribution than *P. asplenioides,* from which it has been separated

only recently. Since the plant was confused with *P. asplenioides* for so many decades, its actual range is in considerable doubt. According to S. Arnell (*loc. cit.*) it occurs in "shady and moist conifer forest" . . . and does not ascend above the forest limit, *i.e.,* is absent from alpine and arctic-alpine areas. This apparently, is one of the most marked differentiating features from *P. arctica,* a taxon of the *P. asplenioides* complex that is hardly more sharply defined than *P. major.*

P. major supposedly occurs from the Mediterranean (Como Sea) to France (Dep. Manche, near Cherbourg) to England and Ireland (Macvicar), northward to Finland and the adjacent portions of Russia.

In North America, a report from Maine (Parlin, 1939) cannot be considered authentic; however, the following collections from Alaska, all of which are in the Yale herbarium as *P. asplenioides,* are possibly assignable to *P. major* on the basis of cell size. These plants, with copiously dentate leaves, represent a phase of the species superficially identical to a large *P. asplenioides,* or else are dense-leaved with conspicuously postically secund leaves (near *P. asplenioides* "var. *devexa*" in form); they possess larger leaf cells, which range in the leaf-middle from 30-33 μ wide or, at times, are even larger.

ALASKA: Tam Gas Harbor, Annette Island (*Frye* 130!; with perianths; plants superficially similar to var. *devexa* of *P. asplenioides, i.e.,* erect in growth, strongly dentate-leaved, the dense leaves somewhat appressed when dry, suberect even when moist, quite postically secund; the pellucid median cells *ca.* (32) 33-36 x 38-45 μ, with slightly bulging trigones); Augustine Bay (*Frye* 544!; median cells 30-35, locally to 37-38 μ wide); St. John's Harbor, Zarembo I., in soggy soil beside mountain streamlet (*Frye* 246; median cells 32-36 μ wide). Very similar is a plant from just NW. of Mt. Chamberlin, Franklin Mts., Brooks Range, Schrader Lake-Peters Lake Area, 3000 ft. (*Steere* 18817; mod. *integrifolia*). This may represent *P. arctica.*

[These plants occur in the same general region with smaller plants, referable to *P. satoi* (see p. 158), that are equally fertile and have leaf cells only *ca.* 25 μ wide medially: Port Alice (*Frye* 724, c. per.!); Nitrofania Bay (*G. B. Rigg* 1219!); St. John's Harbor, Zarembo I. (*Frye* 230!; c. per.; a mod. *dentata* close to var. *devexa,* the median cells only 22-25 μ wide). The fact that they occur in the same localities (*e.g.,* St. John's Harbor, Zarembo I.) suggests that the large and small-celled plants must be genetically distinct, even though American students have considered them to be identical and representative of *P. asplenioides.*

In addition to the preceding two extremes there occur plants intermediate in cell size, among them: Lake Bay (*Frye* 205!; median cells 28-30, locally 30-32 μ wide); mouth of Hidden Inlet (*Frye* 60!; median cells 28-30 μ wide); Swift's Cannery, Hecate Island (*Frye* 691!; cells 28-32 μ wide). These plants, although not wholly typical, I believe are best retained in *P. asplenioides.*]

The relationships of the large-celled plants cited above to European *P. major* need investigation. They fail to attain the very robust size of *P. major,* rarely attaining a length in excess of 3-5 cm on the simple or subsimple aerial shoots. The gamut of variation appears to parallel almost completely that of *P. asplenioides;* hence the plants

can only be separated from the latter by cell size and by an inconstant tendency, when dry, to be slightly nitid.

These large-celled plants, which closely agree with *P. major*, are also difficult to separate from *P. arctica*. As is pointed out under the latter, *P. arctica* exists in two extremes, the typical, reniform- and appressed-leaved phase, and a phase with ovate or oval leaves that are more or less patent laterally, in antical aspect (var. *intermedia*). Typically, the latter is a larger, more robust plant than *P. arctica* s. str., and, in this respect, as well as in cell-size approaches *P. major*. The distinctions between *P. major* and *P. arctica* var. *intermedia* thus are slight (the lack of dentition of the leaves, usually; the somewhat larger and even more pellucid cells), and may not warrant two species. However, *P. arctica intermedia* and *P. arctica* s. str., in turn, appear very closely allied. These relationships are clear from the following diagram:

$$
\begin{tikzcd}
\text{(A)} & \text{(B)} \\
\textit{P. arctica}\text{ var. }\textit{intermedia} \arrow[r] & \textit{P. arctica}\text{ s. str.} \\
\textit{P. major} \arrow[u] & \\
\textit{P. asplenioides}\text{ s. str.} \arrow[u] \arrow[r] & \textit{P. a.}\text{ var. }\textit{subarctica} \arrow[uu] \\
\textit{P. satoi} \arrow[u] &
\end{tikzcd}
$$

From this diagram it is obvious that *P. major* occupies a somewhat unstable middle ground between typical *P. asplenioides*, and between the large, patent leaved plant distinguished on a succeeding page as *P. arctica* var. *intermedia*. The taxa in column *A* all have the normal, plagiochiloid facies, with the ovate leaves more or less patent and/or somewhat postically secund; the plants in column *B* have reniform, *Nardia compressa*-like leaves that are erect-appressed and antically connivent. This diagram is also so arranged that the taxa on top are large-celled, those on the bottom, small-celled. On this basis, again, the intermediate position of *P. major* is clear. Much more work is needed to establish any sound phylogenetic arrangement of the members of this complex. They have all arisen from a single antecedent species, presumably most similar to *P. asplenioides* s. str. Furthermore, they fail to diverge enough from the latter to have achieved the status of well-marked species; it is quite possible that treatment of all of them as races of a single species should be attempted. Arguments against this are based chiefly on the fact that some members (such as *P. major*) have a relatively limited geographical range. Nevertheless, study of a series of collections from northwestern North America (see Table I) suggests that cell-size variation does not follow a simple bimodal curve. It is very questionable whether recognition of species, in this complex, on the sole basis of cell-size and plant vigor is justified. It is, furthermore, unclear whether the large-celled Alaskan plants I reluctantly refer to *P. major* are genetically similar, or represent a parallel phase evolved independently.

P. major appears to be closely allied to a Formosan plant, described by Horikawa (1934, p. 161, pl. 12, figs. 1-15) as *P. magnifolia.* This plant is even larger (to 12 mm wide x 10 cm long), with leaves up to 4 x 7 mm, and has the apical cells 38 μ and the median 48 x 56 μ. It is possible that a polyploid series is involved here, with *P. asplenioides* haploid, *P. major* diploid, and *P. magnifolia* showing an even higher level of polyploidy. Carl (1931) already suggested a polyploid origin of *P. major;* this hypothesis awaits confirmation. Certainly, *P. magnifolia,* with its relatively enormous cells and exceedingly robust size represents a member of this same holarctic complex.

PLAGIOCHILA ARCTICA Bryhn et Kaal.

Figs. 10 B, 11

Plagiochila arctica Bryhn and Kaalaas, Rept. Second Norwegian Arct. Exped. in the "Fram" 1898-1902, 11:41, 1906; Arnell, Arkiv f. Bot. 13:19, pl. 1, figs. 12-21, 1913.

Chiloscyphus polyanthus Frye and Clark, The Bryologist 49:59, and 51:253, 1946, 1948 (at least in part; fide Persson, The Bryologist 55:8, 1952; not of Corda).

Plant identical in facies to *P. asplenioides* var. *subarctica,* yellow-green, *strongly laterally compressed, erect and caespitose,* 10-20 (25) mm high x 1.25-1.8 (2.2) mm wide (lateral aspect). Stems *ca.* 250-310 μ in diameter, the cortex rather poorly developed, consisting *of only 2 layers* of somewhat smaller, brownish, moderately thick-walled cells, *ca.* 20-23 μ to 22-33 μ broad x 42-62 (75) μ long; medullary cells up to nearly twice that in diameter, 25-36 x (90) 100-165 μ long, pellucid and leptodermous; branching wholly intercalary and from lower end of axils of leaves, *the branches often negatively phototropic, reduced-leaved, stolon-like,* or often arching upward and becoming leafy (then frequently with a stolon near base of the branch); rhizoids abundant on stolons, rare elsewhere. *Leaves broadly reniform to reniform-rotundate,* from 1500 μ wide x 1050 μ long to 1620-1675 μ wide × 1175-1200 μ long (length *ca. 0.7-0.8 the width*), *nearly flat, or with antical margin very slightly reflexed, not markedly adaxially convex,* the apices only rarely reflexed, usually *erect-appressed and somewhat antically secund,* the shoots appearing strongly laterally compressed; *margins* entire to obscurely sinuous, *only occasionally with a few minute teeth. Cells very large and pellucid,* the marginal and apical (29) 30-36 μ, the median 38-44 x 40-46 μ, the median basal (29) 32-40 μ x 40-60 μ, with thin to slightly thickened walls and small to moderate, non-bulging trigones; *oil-bodies numerous, 15-24 per cell,* spindle-shaped to elliptical to oval, coarsely segmented, 3 x 5-7 μ to 4-5 x 5-8 μ, a few to 5 x 9 μ. Underleaves obsolete.

Gynoecia *often on more or less abbreviated lateral branches,* swiftly becoming large-leaved from a small-leaved basal portion, *strongly complanate, the bracts and subinvolucral leaves rotund-ovate to reniform-ovate,* often broadly rounded at both antical and postical bases and *sometimes somewhat cordate, entire-margined.* Perianth in lateral profile *obdeltoid-obcampanulate, relatively short, hardly emer-*

gent from between the appressed bracts, wide at the rounded mouth, the antical and postical keels unwinged, *hardly longer to 1.2-1.35* x as *long as the mouth is wide; mouth entire.* (Diagnosis of female plant from *Steere* 17944).

Type.—Havnefjord, on the south shore of Ellesmere Island (*Simmons*).

Distribution.—Evidently a strictly arctic polyploid derivative of *P. asplenioides.* The latter occurs northward as far or nearly as far as *P. arctica* (the two occur together in northernmost Ellesmere Island, and at Unalaska, Aleutian Islands, Alaska, for instance), so there appears to be good reason for considering them as specifically distinct —since they have all the attributes of biologically distinct species.

P. arctica is known from Greenland and Ellesmere Island westward to the Aleutian Islands and (questionably) into Siberia (Lena R., at Lat. N. 70° 30′ 72″). The report of the material from Scandinavia is based on material determined by Kaalaas, *in* Bryhn (Nyt. Mag. Naturvid. 46: 41, 1907), but Joergensen (1934) describes this as a new variety, var. *subarctica of P. asplenioides.* There are probably reports of *P. arctica* from this general region which have been erroneously listed under *P. asplenioides* in the literature.

ALASKA: King Cove, Alaska Peninsula (July 25, 1932, *W. J. Eyerdam;* among *Saxifraga serpyllifolia;* mod. *densifolia-latifolia-integrifolia-mesoderma*); Unalaska (Aug. 30, 1932, *W. J. Eyerdam;* among *Carex circinata;* mod. *densifolia-latifolia-erectifolia-integrifolia-pachyderma*); Unalaska (July 22, 1938, *J. P. Anderson;* among *Antennaria monocephala;* mod. *latifolia-integrifolia-mesoderma*); Unalaska (July 19, 1932, *E. Hultén;* among *Salix reticulata;* mod. *parvifolia-meso-vel pachyderma-integrifolia*); Unalaska (June 14, 1932, *W. J. Eyerdam;* among *Antennaria monocephala;* mod. *latifolia-densifolia-denticulata-meso-vel pachyderma*); Attu I. (*Hardy;* listed by Frye and Clark as *Chiloscyphus polyanthus;* see Persson, 1952, p. 8); Yakutat Bay (Clark and Frye, 1949); Sitka (Persson, 1946); Juneau (Persson, 1946); Skagway (Persson, 1946); Dolgoi I., W. Pacific Coast (Persson, 1946); Akutan, Aleutian Isls. (Persson, 1946); Umnak I., Aleutian Isls. (Persson, 1946); Driftwood Camp, near headwaters of Utukok R., N. slope of De Long Mts., *ca.* 68°53′ N. and 161° 10′ W. (*Steere* 16897!, 16855!, 16695!, 16779!, 16821!, 16855!); Schrader, Lake-Peters Lake area, NW. of Mt. Chamberlain, Franklin Mts., Brooks Range, 69°22′ N. and 145°03′ W., *ca.* 3000 ft. (*Steere* 18831!); Umiat, Colville R., *ca.* 69°23′ N., and 152°10′ W. (*Steere* 17149!; typical, appressed-leaved but robust phase); Attu Island (*fide* Clark and Frye, 1949); on steep, wet, north-facing slope, between Mt. Araga and Smith Lakes, just W. of Etivluk R., Endicott Mts., Brooks Range, *ca.* 68°43′ N. and 156°30′ W., 2000 ft. (*Steere* 17944; typical, c. per.!); Meade R. Camp, *ca.* 70°39′ N. and 156°55′ W. (*Steere* 15851!; a form with leaves ovate to rotund-ovate or rotund-reniform, ± appressed to erect-spreading; perianth mouth entire, but bracts obscurely paucidentate).

ELLESMERE ISLAND: East edge of U.S. Range, 2000-2200 ft., 9-10 mi. due W. of Mt. Olga, 82°24′ N., 65°20-30′ W. (*Schuster* 35599c, 35570); ¼ mi. N. of Mt. Pullen, 5 mi. S. of Alert, 82°26′ N., 62°15′ W., northeast Ellesmere I. (*Schuster* 35376, 35377, 35329); N. base of Mt. Pullen, *ca.* 82°25′ N. (*Schuster* 35103g); E. face of Mt. Pullen, 5 mi. S. of Alert (*Schuster* 35338, 35349); NW. slope of The Dean, 5-6 mi. SE. of Alert, 82°25′ N., 62° W.

(*Schuster* 35191); Cape Rutherford (*Simmons* 669! *and* 781!). Also reported from Hayes Sound region: Beitstad Fiord and Cape Rutherford; South Coast: Fram, Harbour and Goose Fiords; West Coast: Reindeer Cove (Bryhn, 1907). DEVON ISLAND, NORTH KENT ISLAND (Bryhn, 1907). N.W. GREENLAND: Thule, 76°30′ — in tufts of *Aulacomium turgidum*.

Ecology.—Apparently a widely distributed species in the Arctic with as wide a tolerance of environmental conditions as has *P. asplenioides* at lower latitudes, judging from the wide range of vascular plants at whose bases it occurs (*Saxifraga serpyllifolia, Lycopodium selago, Plantago, Antennaria monocephala, Salix reticulata, Carex circinata etc.*). Associated Hepaticae are generally *Blepharostoma trichophyllum, Tritomaria quinquedentata, Ptilidium ciliare, Lophozia alpestris major, Scapania simmonsii, Arnellia fennica,* and in the northwest, *Radula polyclada* and *prolifera.*

On the northern coast of Ellesmere Island, at *ca* 82° 24′ N., the species is confined to moist, highly calcareous moss-tundra, in areas otherwise characterized by being "high arctic deserts;" here the plant is associated with some of the same species found with the wholly similar *P. asplenioides subarctica: Lophozia pellucida, L. quadriloba, L. heterocolpa* and its var. *harpanthoides, Blepharostoma trichophyllum brevirete, Scapania polaris, S. gymnostomophila,* as well as with *Cryptocolea imbricata, Anthelia juratzkana, Arnellia fennica, Solenostoma polaris, Tritomaria quinquedentata, Cephaloziella arctica,* and rarely *Gymnomitrium concinnatum.* Almost wholly restricted to areas adjacent to persistent snow banks, or to slopes lying below firn ice-invested hills or mountains, and usually in areas where permafrost remains within 1-4 in. below the surface during the growing season (June 15-August 24 usually).

Differentiation.—The generally subentire or entire leaf-form, the very broadly ovate to suborbicular or rotundate-reniform leaves, and the entire facies suggest various phases of *P. asplenioides.* It is probable that *P. arctica* represents only a polyploid arctic derivative of the latter species, and it can be separated from *asplenioides,* when sterile, only by the larger cell size (see Table I), as well as by the correlated more pellucid appearance of the plants. When fertile, the erect-appressed, often cordate bracts, and the short, included or hardly emergent, perianth is distinctive.

In appearance, as well as the large cell-size, *P. arctica* may approach *P. columbiana* Evs., a species apparently restricted to the Piedmont of southeastern North America. In fact, if the range of the two taxa were contiguous, the writer would hesitate to consider them discrete species. However, in addition to the differences in range, a few morphological peculiarities serve to separate the two taxa: (1) *P. arctica* apparently never bears irregular polymorphic teeth or small lobes; in *P. columbiana* most shoots show at least some leaves thus armed; (2) *P. arctica* frequently has the erect leaves more or less

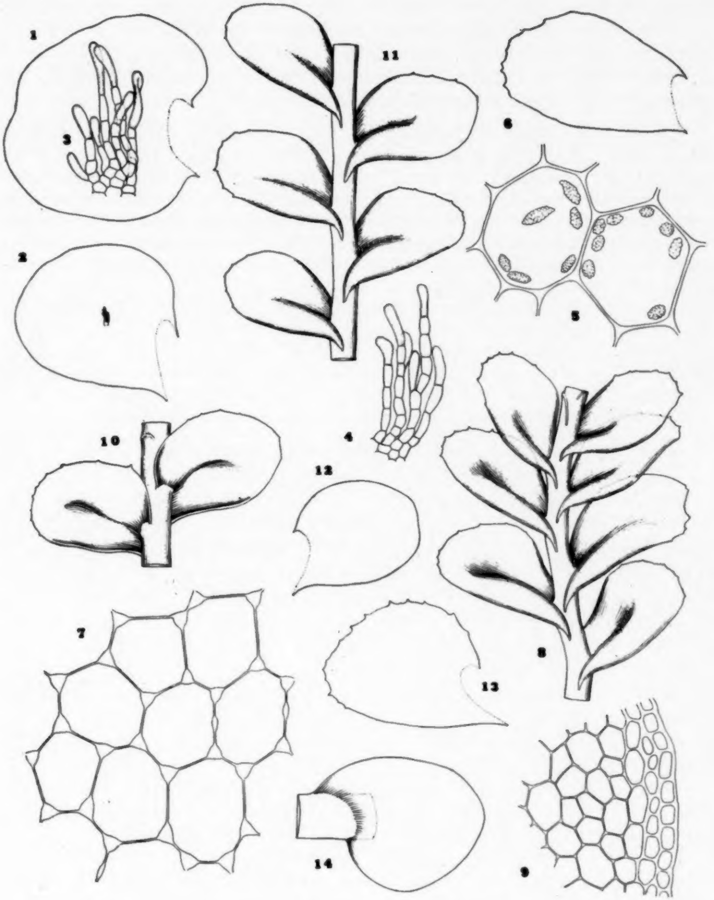

Fig. 11.—*Plagiochila arctica* var. *intermedia* Schuster. 1-2. Two leaves and, in 2, an underleaf (all x 12); 3-4. Underleaves (x 63); 5. Median cells with oil-bodies (x 385); 6. Leaf of plant in fig. 8 (x 12); 7. Median cells (x 275); 8. Shoot-sector (x 9.7); 9. Part of stem cross-section (x 141); 10. Shoot-sector, postical aspect (x 12); 11. Shoot-sector of mod. *laxifolia-angustifolia-subdentata* (x 9.7); 12. Leaf of mod. *parvifolia-integrifolia* (x 15); 13. Leaf of mod. *densifolia-integrifolia* (x 12). (Figs. 1-5 from *Steere* 16897, Driftwood Camp, Alaska; 6-14 from fragmentary collections from Alaska, leg. Persson).

dorsally connivent; in *P. columbiana* they spread widely laterally; (3) the underleaves of *P. arctica* consist of a few minute, contiguous, uniseriate cilia, tipped with hyaline papillae, in *P. columbiana* at least occasional plants produce larger, lamellate underleaves. *P. arctica* also differs from both *P. asplenioides* (exclusive of var. *major*) and *P. columbiana* in the much larger maximal size attained, and in the generally shiny appearance of the dry plants.

The various phases of *P. arctica* may look distressingly different from each other. The rather rare, minutely dentate phases may look like "normal" *P. asplenioides*. By contrast, the typical yellowish-green, dense-leaved forms, with reniform-rotundate, broader than long, erect-appressed leaves have scarcely any resemblance to *Plagiochila*. The flat or concave leaves of such forms, with the antical margin flat and with the consequent lack of the cnemis, give such plants an entirely different facies — suggesting such unrelated taxa as *Nardia compressa* and *Jamesoniella carringtonii*.

Associated with a caespitose pattern of growth under "difficult" conditions, the perianth of this species is much broader and shorter than in *P. asplenioides*. In the examined fertile material it is virtually or quite included, only rarely about one fourth emergent, hence difficult to find. The bracts are often more ovate than the subinvolucral leaves, and may average slightly longer than wide even when ordinary leaves are rotundate or reniform and wider than long.

The typical plant differs considerably from some forms of *P. arctica* from Alaska (some of which were reported as this species by Persson). Although it is possible that the typical plant is merely a dwarf, imbricate-leaved, caespitose modification (mod, *densifolia-latifolia-parvifolia-integrifolia*) of a more optimal *P. arctica*, this does not appear to be the case, because of the more numerous oil-bodies of the typical plant from Ellesmere Island (compared to Alaskan material of *P. arctica*). Typical *P. arctica* has approximately twice as many oil-bodies per cell as the much smaller-celled plant from the same area of Ellesmere Island which is referred to *P. asplenioides subarctica*. However, the leaves are very similar in shape, averaging much broader than long, and the two plants agree in facies. Indeed, they can only be separated by microscopic examination. The two plants agree particularly in the strongly compressed shoots, with somewhat antically connivent leaves, reminiscent of those of *Jamesoniella carringtonii*. They are also strongly similar to each other in that stolons from the lower halves of the leaf axils are very commonly produced.

Variation.—*P. arctica* appears to undergo a more restricted, but almost identical pattern of variation, as does *P. asplenioides*. The similarity in mode of modification is particularly great when material of *P. asplenioides* from the northern edges of its range is compared with *P. arctica*.

In general, variation extends from a hygric extreme, with the following peculiarities: (1) leaves lax, the internodes long; (2) leaves relatively narrow, *ca.* 1.3-1.5 as long as wide, often obovate in shape; (3) leaf-margins often, but not always, more or less dentate; (4) cells with trigones little or not bulging; (5) leaves spreading laterally, usually at an angle of 55-65°, occasionally even wider. In such forms,

the width of the median cells is usually not appreciably wider than in the xeromorphic extremes, and may average only 35-39 μ, but the length of the cells (associated with the increased leaf-length) is often unusually great (48-52, or even 60 μ long medially, 60-72 μ long basally).

This hygric extreme, with relatively elongate leaves, is relatively rare, and is connected by an imperceptible gradient to an xeromorphic extreme, with the following features: (1) leaves dense, often suberect, the internodes short; (2) leaves relatively broad, always widest well below middle, often suborbicular, from ca. 1.1 to 0.95 as long as wide; (3) leaf-margins usually entire, but occasionally denticulate; (4) cells with pronounced, bulging trigones. Such xeric forms may have the cells appearing slightly smaller, and always distinctly shorter, with the variation from *ca.* 33-40, often only 33-36 μ wide x 35-42 μ long medially, while at base they may be only 34-43, occasionally 46-52 μ long. Midway between these two extremes stand the relatively robust phases of the species. In the more mesic phases (typified by *Steere* 16897 from the Brooks Range, Alaska) the leaves are contiguous to weakly imbricate, spread laterally, and average about as broad as long (2250 μ x 2250 μ) or barely longer than broad. In the most robust phase, grown evidently under optimal conditions (mod. *latifolia-integrifolia-densifolia*), typified by such specimens as *Steere* 17149 (Umiat and vicinity, Alaska) the plants become appressed-leaved. Here the leaves are erect-appressed to the stem, broadly rotundate to rotundate—reniform with the cnemis not at all developed—the antical margin being essentially plane. The leaves here are commonly 3.2 mm wide x only 2.5 mm long (length: width = *ca.* 0.8:1) up to 3.4 mm wide x 2.6 mm long (length: width = 0.77:1). The cells in this phase are of maximal size, the marginal averaging *ca.* 35 μ; the median *ca.* 35-44 μ wide, and bear only small to medium-sized trigones. In the experience of the writer, such robust phases of *P. arctica* are very common in the far north, and can be regarded as the "typical" phase of the species. Similar modifications (mod. *latifolia-integrifolia-densifolia*) are produced in the Arctic by *P. asplenioides,* but apparently only by the smaller, xeromorphic phases (*i.e.,* this variation is linked with the mod. *parvifolia*), as is evident on studying *Steere* 17108 (Umiat and vicinity, Alaska). In the latter material of *P. asplenioides,* the leaves are only 1100-1125 μ wide x 750-875 μ long! These plants represent *P. asplenioides* var. *subarctica* Joerg.

The above observations are based on limited knowledge of the species in the field. Undoubtedly further collections and detailed field studies will show a wider range in variation. However, several differences appear to stand out in the pattern of variation, between this species and *P. asplenioides:* (1) The range in variation in cell size at all times runs far in excess of the range in *P. asplenioides.* (2) The margins of the leaves appear unable to produce the numerous marginal teeth characteristic of many forms of *P. asplenioides.* In almost all instances (except for a few hygric extremes seen) the leaves were nearly or quite entire. It should be emphasized that Frye and Clark attempt to separate *P. arctica* from *P. asplenioides* on the basis of the entire leaves of

the former, *vs.* dentate leaves of the latter. As Persson (1952, p. 8) has pointed out, these authors appeared to have quite misunderstood this species, reporting *P. asplenioides* as *P. arctica* (1945) and (1946) mistaking true *P. arctica* for the unrelated *Chiloscyphus polyanthus!* (3) The plants always appear to be much more translucent or pellucid than in *P. asplenioides.*

Although one may assume, with Persson, that *P. arctica* is a polyploid derivative of *P. asplenioides* and therefore hardly merits specific rank, the extraordinary variability of *P. asplenioides* makes it desirable to maintain *P. arctica* as a species, at least for the time being. Furthermore, in my experience, the large-celled polyploids usually bear more numerous oil-bodies per cell. This does not necessarily appear to be the case. In Alaskan material (*Steere* 16897), identical with Alaskan plants referred by Persson to *P. arctica,* with the median cells *ca.* 38-40 μ wide x 40-48 μ long there were only 4-8 (10) oil-bodies per cell, much as in normal *P. asplenioides.* By contrast, typical phases of *P. arctica,* from Ellesmere Island, differ in possessing numerous oil-bodies, ranging from 15-24 per cell. This suggests that *P. arctica,* as circumscribed by Persson, *i.e.,* including both lax-leaved phases with spreading, ovate leaves and dense-leaved phases with broad, reniform leaves, is still genetically polytypic. If we are to recognize varieties in the species, the "typical" phase of the species must be considered to be the reniform and appressed-leaved extreme, in which I have found numerous oil-bodies per cell. The lax-leaved, and relatively narrow-leaved phase with fewer oil-bodies per cell should then be separated varietally, as per the subjoined key:

KEY TO VARIETIES OF P. ARCTICA

1. Leaves erect-appressed, somewhat antically connivent, broadly rotundate-reniform to subreniform, 1.1-1.3 × as wide as long on mature shoots, edentate; cells each with 15-24 oil-bodies. .... *P. arctica,* typical
1. Leaves laterally more or less patent, not antically connivent, either postically secund or laterally patent, oval to ovate to subrotundate, usually 0.95-1.5 × as long as wide, varying from entire-margined to sparingly or copiously dentate, never strongly reniform in shape; cells each with 4-8 (10) oil-bodies per cell. .... *P. arctica* var. *intermedia*

Plagiochila arctica var. intermedia var. n.

P. arcticae similis; differt: folia late ovata, patentia; corpora oleifera 4-8 (10). Typus: Brooks Range, Alaska, 68° 53′ N., 161° 10′ W. *Steere* 16897).

Plants in patches or isolated and creeping over other bryophytes, yellowish- or whitish-green to greenish, *rather pellucid, nitid when dry.* Shoots (with leaves) 3-5.5 (6.5) mm wide, subsimple to irregularly monopodially branched, the branches all intercalary. Stems 13-15 (18) cells high, *ca.* 450-500 (575) μ wide x 345-360 (425) μ high; cortex in 2, rarely locally in 3 layers, the cortical cells somewhat tangentially flattened, moderately thick-walled, 20-25 μ (tangentially measured) wide x 68-100, occasionally 80-112 μ long, the walls yellowish to golden-brown; medullary cells suddenly considerably larger than cortical, becoming *ca.* 27-33 μ, to a maximum of 32-36 μ in diameter medially, colorless, thin-walled, the corners little thickened. Rhizoids absent or virtually so on leafy shoots. *Leaves variable, usually laterally patent both when dry and moist,* rarely antically connivent, *undergoing strong variation in shape;* in lax, large (mesic to mesic-

hygric) forms *ovate to obovate,* narrowed rather strongly basally, *ca.* 1425 μ wide x 2100 μ long (1.4-1.5 × as long as wide); in robust mesic forms rotundate and sometimes becoming broader than long, to 3200-3400 μ wide x 2500 μ long; in xeromorphic forms much smaller, ovate *to orbicular,* broad, strongly narrowed basally, *ca.* 1575 μ wide x 1675 μ long (1.0-1.1 × as long as wide) to an extreme of 1500 μ wide x 1450 μ long (*ca.* 0.95 as long as wide). Antical margin plane (dense-leaved forms) or more or less strongly reflexed for 0.5-0.8 its length, when flattened out varying from slightly arched (large-leaved forms) to strongly convexly arched (xeromorphic forms), edentate, basally rather long-decurrent; postical margin moderately (large-leaved forms) to very strongly, nearly semicircularly, arched (xeromorphic forms), the postical base virtually non-decurrent to very short-decurrent, not or scarcely reflexed. *Leaf-margins usually edentate* (most xeromorphic forms) *to somewhat irregularly and minutely, sparsely dentate* (most lax-leaved, hygromorphic forms), the teeth 6-15, usually 1-2 cells long and 1-2 cells wide at base, the terminal cell nearly isosceles-triangular. Leaves little secund postically, spreading laterally (mesic and hygric forms) to suberect or nearly erect in dorsal aspect (spreading at less than 45°) in xeromorphic forms, varying from distant (hygric) to rather closely imbricate (xeric forms). Cells usually with distinct, sometimes with rather large and bulging trigones (mod. *pachyderma* frequent in nature), the walls thin, colorless to, occasionally, faintly yellowish; cuticle smooth to almost imperceptibly roughened; *cells of margin of leaf-apex* 23-35 x 30-37 μ, collenchymatous like inner cells or ± thick-walled (but often without trace of equally thick-walled border); *median cells* 33-42 (44) μ wide x 36-45, occasionally 45-54 μ long; cells on middle of postical margin 24-36 μ wide x 34-42, occasionally 42-48 μ long; cells of middle of base *ca.* 32-36 (40) x 38-50, occasionally 50-72 μ long. Oil-bodies segmented, usually ellipsoid to fusiform and 4 x 7.5 to 5 x 11 μ, occasionally spherical in some cells and 4.5-5 μ, *occurring mostly 4-8 (10) per median cell, their size relatively small,* for cell area, and chloroplasts relatively small and few for cell size; *cells as a consequence relatively pellucid.*

Type.—Brooks Range, Alaska, at Driftwood Camp near headwaters of Utukok R., N. slope of De Long Mts., *ca.* 68°53′ N. and 161°10′ W. (*Steere* 16897); type plants in collection of Stanford University, and in herbarium of author.

Distribution.—Known, so far, only from a series of plants collected in Alaska. Of the Alaskan collections cited under *P. arctica* s. lat. several approach the var. *intermedia.* The following collections are all assignable to var. *intermedia.*

UNALASKA: (*W. A. Setchell,* 1030! as *P. asplenioides* in herb. Y, det. Evans); Driftwood Camp, near headwaters of Utukok R., N. slope of De Long Mts., *ca.* 68°53′ N. and 161°10′ W. (*Steere* 16855!; an ovate-leaved plant approaching a large typical *P. arctica,* clearly transitional; leaves appressed and antically connivent); Unalaska, Aleutian Isls. (June, 1932, *E. Hultén!*; among

Plantago macrocarpa; mod. *laxifolia-angustifolia-patulifolia-subintegrifolia*); Unalaska (May, 1932, *Eyerdam!,* among *Lycopodium selago;* mod. *laxifolia-angustifolia-pachyderma*).

As is obvious from the discussion under *P. arctica* s. lat., the present form, with more or less patent to postically secund leaves that are not appreciably wider than long, represents the form most nearly analogous to "typical" *P. asplenioides,* with forms of which it may be superficially identical. Inversely, *P. arctica,* typical, is superficially indistinguishable from *P. asplenioides* var. *subarctica.*

PLAGIOCHILA SATOI Hattori

Fig. 12

Plagiochila satoi Hattori, Bot. Mag. (Tokyo) 57:361, fig. 6, 1943; Hattori, J. Hattori Bot. Lab. 10:68, 1953 (oil-bodies described); Inoue, J. Hattori Bot. Lab. 19:51, fig. VIII:12-21 and fig. IX, 1958.

Plagiochila hakkodensis var. *dentosa* Hattori, J. Jap. Bot. 25(7):139, fig. 56, 1950.

Plagiochila dentosa Hattori, J. Hattori Bot. Lab. No. 12:84, 1954.

Plagiochila japonomontana Hattori, *in* M. Sato, Flora of Mts. Asahi, Gassan and Chokai (N. Japan). Bull. Yamagata Agr. Coll. No. 1:102, 1949.

Plants similar to a small form of *P. asplenioides,* only 1.5-2.5 cm high, caespitose in growth, freely fertile. Shoots (1.5) 1.8-2.4 (2.6) mm wide, the aerial shoots usually simple or with isolated branches or stolons from near base; usually with subfloral innovations. Stems olive-brown to brown, rigid, 200-280 μ in diameter; cortex only 2-3-stratose, of cells 10-13 μ in diam. Leaves varying from 1125-1325 μ long x 1275-1425 μ wide (0.97 to 1.25 $\times$ as broad as long; Alaskan materials) to 1337-1460 μ long x 1400-1450 μ wide (0.98-1.05 $\times$ as broad as long; typical Japanese plants) up to a maximum of 2000-2150 μ long x 1800-1950 μ wide (0.83-0.88 as broad as long; optimal Japanese plants, *Inoue* 6423!), varying from very broadly ovate to subrotundate; leaves obliquely laterally patent but *usually strongly postically deflexed and postically* concave, mostly *broadly ovate to suborbicular,* short-decurrent postically, long-decurrent antically, *broadly rounded at apex,* the weakly or moderately arched *antical margin strongly reflexed nearly to the leaf* apex (usually so strongly so as to be almost tubularly convolute; the dissected leaves normally cannot be flattened under the cover glass); postical margin strongly arched, evenly rounded into the apex, the *entire postical margin* (except sometimes for a very short basal strip) *and the apex very closely and strongly spinose-dentate to spinose-denticulate,* the teeth *ca.* 19-25 (34) (with an additional 2-5 [8] oblique, lower, serrate teeth on distal 0.5-0.7 of the convolute antical margin; thus *with a total of ca.* [15] *20-30* [42] *marginal teeth*), rarely entire-margined. *Teeth very strong* in relation to the leaf-size, somewhat variable in size, *almost never totally suppressed,* ranging from 1-2 cells wide at base x 2-3 cells high *up to 3-4 cells wide x 5-7* (*8*) *cells long;* terminal cells slightly elongated, *up to twice as long as high,* the subterminal cells *little or not longer than broad* (usually 17-21 (23) μ wide x 17-24 μ long); teeth often very narrow, formed of commonly 2-4, *occasionally 5 super-*

imposed single cells. Cells of leaves very small, smaller than in other species of the Sectio Asplenioides; the submarginal and subapical (within the marginal row) only 18-21 x (18) 19-23 μ; the median (21) 22-26 (27-28) x 24-28 (30-32) μ, almost isodiametric and usually hexagonal; the cells at base, along midline of leaf, *forming an ill-defined group of somewhat elongate, often somewhat thick-walled cells,* ranging from 17-24 (25) x 32-48 (65) μ, but these *not forming a vitta;* marginal 1-3 cell-rows commonly somewhat, often conspicuously, thick-walled; median cells relatively thin-walled and usually with small to barely bulging trigones; basal cells often evenly thick-walled; cuticle smooth. Oil-bodies (fo. *subintegerrima* Hattori) 5-7 (10) per cell, varying from 4-4.5 x 6-7 μ, a few spherical and 4 μ, occasionally to 3.5-4 x 9-12 μ, distinctly segmented but sometimes obscurely so (then superficially homogeneous). Underleaves vestigial, of a few obscure cilia tipped by slime papillae. *Asexual reproduction absent.*

Dioecious. Androecia as in *P. asplenioides;* bracts 2-androus. Gynoecia terminal on leading shoots, with 1 subfloral innovation or free of innovations. Bracts similar to leaves, often suberect to erect (especially when perianth juvenile), similar to leaves in shape, tending to be even more sharply spinose-dentate, and the antical margin even more convolute, and more freely dentate. Perianth without either keel winged, subequal, 2-2.8 mm long x 1.3-1.6 mm wide at mouth, the subtruncate mouth very closely, rather strongly, spinose-dentate. Spores *ca.* 17 μ; elaters 2-spiral, *ca.* 10 μ in diameter.

Type.—Japan (Mt. Jonen, Nagano Pref., Honshu, *Hattori* 1342).

Distribution.—Previously known only from Japan, from where I have seen the following specimens: Mt. Bunagadake, Shiga Pref. (*Kodama* 9929!); Mt. Hafu, Chichibu, Saitama Pref., 2300 m. (*H. Inoue* 3961!); Shiraiwa in Chichibu Mts., Saitama Pref., 1800 m. (*H. Inoue* 7220!; fo. *japonomontana*); Ohoyama in Chichibu Mts., Saitama Pref., 2200 m. (*H. Inoue* 6423!; a large phase); Kawakamimura, Nagano Pref., 1300 m. (*H. Inoue* 5338!); Mt. Hakkoda, Aomori Pref., 1400 m. (*M. Hara* 8141!); Sanpozan of Chichibu Mts., Otaki, Saitama Co., 2380 m. (*Shimizu!*; No. 281 of Hattori's Hep. Jap., issued as "*Plagiochila dentosa* Hatt.").

Recurring in a slightly deviant phase, in coastal southeastern Alaska, as follows:

ALASKA: Port Alice, on wet rocks (*Frye* 728!; a trace, among *Plagiochila rhizophora* subsp. *confusa;* with *Metzgeria hamata, Riccardia multifida*); on wet rocks, Port Alice (*Frye* 724!; with perianths, a rather large phase); St. John Harbor, Zarembo Island, on log, 500 ft. (*Frye* 230!); Nichols Bay, on tree-base, June 8, 1913 (*Frye* 392a!; in Univ. Wash. herbarium, as "Topotype of *Plagiochila alaskana*" among *Metzgeria conjugata*). The preceding collections, except for the last, were all determined by Evans (1914, p. 590) as *P. asplenioides* and form part of the basis for the reports of *P. asplenioides* from Alaska.

Ecology.—In Japan, the plant appears to be exclusively montane

and is found on the bases of tree trunks (*e.g.*, of *Tsuga* and of *Fagus crenata*) and on moist rocks. On rocks it is variously reported from "moist . . . quartz-diorite . . . ledges by mountain stream," and from "granitic rocks" in "coniferous forest." The plant here occurs at altitudes chiefly of from 900-2400 meters, although descending to 400 meters in Hokkaido. The few Alaskan collections are from decaying logs and from wet rocks, on which the species may grow "among mosses" or with *Metzgeria hamata* and *Riccardia multifida,* more rarely on tree-bases with *Metzgeria conjugata.*

It is of some interest that the species is habitually quite small, forming tufts or sods rarely exceeding 2-2.5 cm in height. This appears to be totally irrespective of environment.

Variation and Differentiation.—*P. satoi* is superficially hardly distinguishable from both *P. asplenioides* and *P. ovalifolia.* It is a species of the Sectio Asplenioides characterized by (a) small maximal size, the shoots usually averaging only 1.8-2.4 mm wide; (b) the broadly ovate-rotundate, almost constantly postically deflexed leaves, giving the plants the facies of a small *P. asplenioides* var. *devexa;* (c) the strongly, often convolutely deflexed antical leaf-margins; (d) the almost constantly strongly but regularly toothed leaf-margins, the dentition becoming even sharper toward the apices of the female shoots; (e) small leaf-cells, in the Alaskan plants the subapical and submarginal 18-21 x (18) 19-23 μ; the median (22) 23-25 (27) x 24-28 μ; the basal often only 17-21 x 32-48 μ. According to Inoue (1958) the cell-size may exceed these measurements.

The species is very closely related to *P. asplenioides,* but the latter species never develops as coarse dentition, even on the most robust and optimal phases (and certainly never on small phases that approach the "normal" phases of *P. satoi*). *P. satoi* and *P. asplenioides* are the small-celled extremes of the Sectio Asplenioides. Of the two, *P. satoi* has the smaller leaf-cells. Indeed, in extreme cases this is almost the only criterion that serves to separate *P. satoi* from the more widespread *P. asplenioides,* and it may "fail" (Table I). There is also an ill-defined tendency in *P. satoi* for the basal cells near the leaf-midline to be somewhat elongated, although not forming even a vestigial "vitta"; such elongated cells are never developed in *P. asplenioides,* although the basal cells are admittedly somewhat longer than broad. *P. satoi* also possesses broad leaves, usually with the area above the postical base prominently dilated and arched.

The oriental, typical, phases of *P. satoi* agree in sometimes developing strongly dentate leaves (the upper extremes cited in the diagnosis refer to such teeth); such plants are referred by Inoue (1958) to "fo. *japonomontana* (Hatt.) Inoue." Rarely (fo. *integerrima* Hatt., in Hep. Jap. No. 284; Mt. Kobushi, Chichibu Mts., Saitama Pref., *D. Shimizu!*) the dentition is markedly reduced or virtually lacking. It is noteworthy that the very closely allied, but larger-celled *P. ovalifolia,* which appears to be an East Asiatic vicariad of *P. asplenioides,* is also characterized by the constantly well-developed and often quite

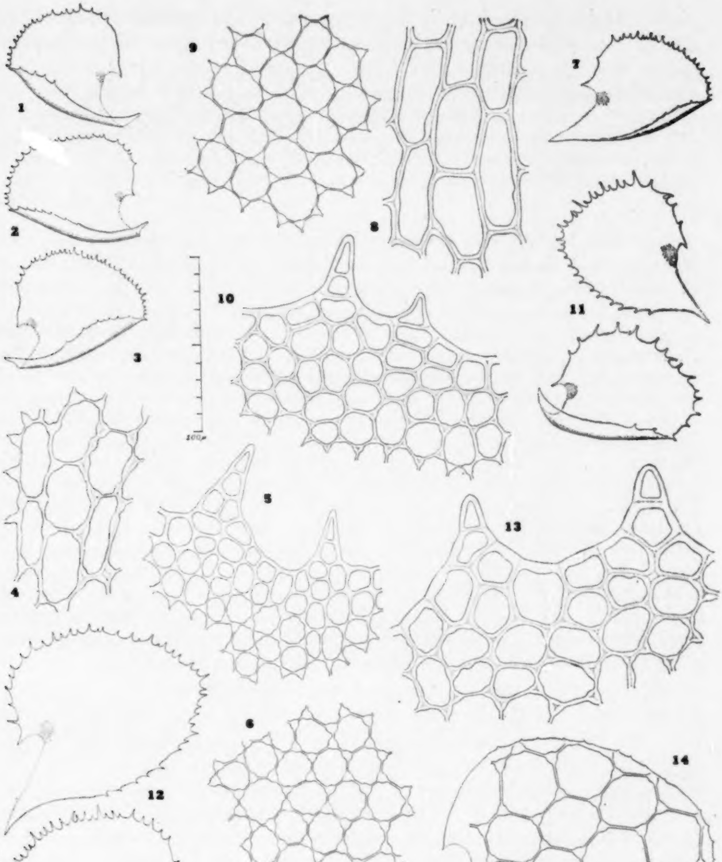

Fig. 12.—*Plagiochila satoi.* 1-3. Leaves (x 12); 4. Cells from leaf-base, along leaf-midline (x 255); 5. Apical cells (x 255); 6. Median cells (x 255); 7. Leaf (x 12); 8. Basal cells along leaf-midline (x 255); 9. Median cells (x 255); 10. Apical cells (x 255); 11-12. Leaves (x 12). *Plagiochila asplenioides* (North Pacific phase). 13. Apical cells (x 255); 14. Leaf (x 12), and drawn within it, median cells (x 255). (Figs. 4-6, 8-10, 13-14 drawn to the scale lying between figs. 3 and 10; figs. 1-3, 7, 11-12, 14 (leaf) drawn to identical scale). (Figs. 1-6, drawn from Alaskan plants, *Frye* 230; 7-10 also from Alaskan plants, *Frye* 724; 11 and 12 from Japanese plants, respectively from *Inoue* 3961 and *Inoue* 6423; 13-14 from a collection [unnumbered] from Queen Charlotte Islands, British Columbia, *Persson,* 1957).

sharp and coarse dentition. Apparently the several East Asiatic derivatives of the more widespread holarctic members of the Asplenioides share a common tendency towards development of coarser dentition (and, inversely, appear unable to develop entire-margined extremes). The Alaskan plants referred to *P. satoi* possess distinct, if less sharp dentition. Similarly, the Alaskan plants of *P. asplenioides* s. lat. possess less sharp dentition than the Japanese plants of *P. ovalifolia* (which Inoue regards as a mere East Asiatic race of *P. asplenioides*).

H. Inoue initially called my attention to the fact that the several Alaskan plants referred here to *P. satoi* must be referred to this species, rather than to *P. asplenioides*. Admittedly, as Inoue writes, in plants that are "not well-developed, as in *Frye* 728 or 724, this species [*i.e.*, *P. satoi*] is hardly separable from a juvenile form of the *P. asplenioides-ovalifolia* [complex]. I examined . . . typical . . . leaves among the fragments . . . in Frye's material." The synonymy is based on the statements (in litt.) of Inoue, who has devoted a special study (Inoue, 1958) to this very difficult complex.

In Alaska, where the *P. asplenioides* complex is particularly variable, I have found plants with the cells of three or possibly four basic sizes: large-celled extremes (*P. arctica*); medium-celled plants (*P. asplenioides* and, possibly forming a weakly differentiated size-class, ? *P. major*); and small-celled plants (*P. satoi*). All three (or four?) extremes had been confused under the portmanteau "species" *P. asplenioides* s. lat. Only the separation of plants of *P. satoi* from *P. asplenioides* is apt to prove difficult; the other two taxa have much larger leaf-cells. The Alaskan plants I refer to *P. satoi* have the median cells only *ca.* 23-25 x 24-28 μ, *on an average* (measuring series of cells); this is also true of the Japanese plants I have studied. Inoue, perhaps incorrectly, gives the median cells more variable in size: 21- 30 μ x 25-34 μ. This measurement probably includes isolated extreme cells.

In the Japanese specimens I have studied there is a marked tendency for the leaves to produce very strong marginal teeth, which with few exceptions, are elaborated to a gradually diminished degree along the antical, deflexed leaf-margins as well. In the typical phases, with "normal-sized" leaves *i.e.*, 1.25-1.5 mm long, the marginal teeth average 18-32 per leaf. The luxuriant, somewhat atypical plants of *Inoue* 6423, with the leaves ranging from 1.65-2.0, occasionally to 2.15 mm long, possess 36-42 teeth per leaf. In all instances seen, a reduction in *number* of teeth is not accompanied by a reduction in *size*. By contrast, the Alaskan plants studied (*Frye* 724, 230), although typical in size and form of leaves (leaves 1.15-1.35 mm long) possess much finer dentition of the leaves than much of the Japanese material, the teeth rarely exceeding 3-4 cells high (vs. 5-7, occasionally 8 cells high in Japanese plants). However, the type specimen of *P. satoi* has relatively fine teeth, 1-3 cells high x 1-2 cells wide at base, as is evident from Fig. IX in Inoue (1958), clearly demonstrating that the variability of the Japanese plants encompasses that of the Alaskan plants. The teeth range, in the Alaskan plants, from *ca.* 27-40 per leaf, thus are comparable in frequency to those of much of the Japanese plants. In spite of the disparity in size of the marginal teeth of the leaves, the Alaskan plants are otherwise virtually inseparable from

the Japanese material. They are therefore retained under *P. satoi,* without any attempt at varietal or subspecific recognition.

There appears to be considerable variation in the Japanese populations; Hattori described them under three separate species names within a decade. In the original diagnosis of *P. satoi* the apical cells are described as 14 x 18 μ, the median as 20-24 x 28-30 μ, and the small group of elongated basal cells as 22 x 50-70 μ. In the original diagnosis of *P. hakkodensis* var. *dentosa,* later elevated to the status of a discrete species, the cells are apparently slightly larger: the apical 18 x 21 μ; the median are not described; the basal vary from 33 x 45 μ to 25 x 58 μ to 30 x 67 μ. In *P. japonomontana* the apical cells are described as 17-20 x 20-23 μ; the median as 25-33 x 27-37 μ; the basal as 24-27 x 45-60 μ. The latter plants, at least as regards the median cells, appear to closely approach typical *P. asplenioides.* However, in all of the various phases of this species that I have seen, there is a rather marked difference between the cells of the peripheral, or marginal portions of the leaf (which are much smaller) and the median cells (which are much larger). The diagnosis of the leaf-cells given in the species description is based on the Alaskan plants; it agrees nearly with that of typical *P. satoi,* although the basal cells are less markedly elongated, hence the incipient vitta is hardly distinguishable.

The status of *P. satoi,* as an independent species distinct from *P. asplenioides,* must be regarded as uncertain. Until a thorough, ecological and biometric study of the Asplenioides Complex is undertaken, accompanied by transplant experiments, the taxa segregated from *P. asplenioides* on the basis of cell-size remain of hypothetical value. Their recognition is often a matter of great difficulty, since there appears to be a considerable amount of environmentally-induced variation in cell-size. For example, a collection of *P. asplenioides* from a dry rock wall, Linville Gorge, North Carolina (*Schuster* 28883), in which the leaves are subrotund and unusually strongly dentate, approaches *P. satoi* in cell-size, dentition, leaf-shape and over-all size. The cells in these plants, a mod. *dentata-parvifolia-latifolia-pachyderma* (Table I) and in others from the Southern Appalachians, average smaller than in "*P. asplenioides* subsp. *ovalifolia*" and approach those of *P. satoi.* Indeed, the cell-size falls well within the range quoted for *P. satoi* by Inoue (1958), and definitely outside the cell-size quoted by him for *P. asplenioides.* Yet these plants, in spite of the rather small cells, are clearly *P. asplenioides,* and like all small phases of this species, lack a basal group of elongated leaf-cells. From the preceding it is clear that the data presented in Table I must serve largely as a basis for future, more detailed studies than are possible here. From my study, of admittedly more limited materials than available to Inoue, I believe that it may be possible that (a) *P. satoi* will prove to be a mere subspecies of *P. asplenioides* s. str.; (b) *P. ovalifolia* will prove to be a subspecies of *P. major,* which is somewhat oceanic in range, rather than of *P. asplenioides* to which Inoue refers it. If such an interpretation should prove to be correct, then the Alaskan plants I tentatively refer to *P. major* would form, possibly, a transition between *P. major* and *P. ovalifolia.* Obviously, a detailed biometric study, on a worldwide basis, is called for.

PLAGIOCHILA COLUMBIANA Evans

Figs. 13A, 14

Plagiochila columbiana Evans, Bot. Gaz. 21:189, Pl. XV, figs. 1-10, 1896.

Plants in pure, dull, almost grass-green *flat patches* on rocks or deeper, *loosely prostrate* mats on soil. Shoots simple or sparingly pin-

nately, usually intercalary but *occasionally terminally,* monopodially branched; 1.5-3 cm long, the branches often at right angles to main stems, rarely dichotomously forking. Shoots with leaves (2.6) 3.5-4.0 (5.1) mm wide; plants a pure green, somewhat opaque (rather densely chlorophyllose), the stems sometimes somewhat darker. Stems quite fleshy, to 14-15 cells high, *ca.* 350-430 μ in width, up to 550 μ wide (x 400 μ high); cortical cells in usually 2 strata, 21-25 (occasionally 25-34) μ wide x (55) 65-85 (100) μ long, rather regularly rectangulate and usually 2.5-4 (4.5) as long as wide, of somewhat tangentially flattened, weakly thick-walled, often slightly yellowish-pigmented cells; medullary cells delicate, up to twice the diameter of the cortical cells. Rhizoids short but unusually frequent, *often present to or near to apex of normal leafy shoots,* the individual plants frequently loosely adnate. *Leaves polymorphic, spreading horizontally* in a single plane, widely divergent (75-90°) from stem-apex, not at all postically secund, contiguous to slightly imbricate, characteristically *very broadly orbicular-ovate to quadrate-ovate* (varying from 1680 μ long x 1800 μ wide, and 0.93 as long as wide; to 1700 μ long x 1720 μ wide, and 0.99 as long as wide; to 1800 μ long and wide; to a maximum of *ca.* 1520-1900 μ long x 2000-2050 μ wide and 0.74-0.95 *as long as wide; on the least robust shoots often* 1.05-1.25 *as long as wide*); antical leaf-margin relatively short-decurrent (for *Plagiochila*), somewhat (but not strongly) reflexed for at least 0.5 its length, slightly concave near base but nearly straight or slightly convexly arched above the base; postical base extremely short-decurrent, the postical leaf-bases never approaching the stem-midline (thus with almost all of postical stem-surface evident in surface view), strongly arched but slightly dilated above the base (the *leaf thus widest in its basal fourth*), the postical margin usually edentate, rarely 1-2 or 3 dentate, plane or occasionally weakly reflexed; *apex typically broadly truncate,* the truncate apex *bearing 2-4, occasionally 5-7 scattered, broad but low, irregular teeth* (some of which are usually lobe-like in nature), *but many leaves appearing irregularly shallowly bilobed* (with postical broad and shallow "lobe" often rounded, the antical smaller and coarsely tooth-like); occasional leaves subentire or truncate-retuse at apex, others irregularly repand-dentate, but usually incipiently 2-3-lobed. Ventral stem sectors unusually broad (generally 7-9 cell-rows wide), *usually freely rhizoidous,* typically able to produce only *very small underleaves* (these usually divided virtually to base into 5-7 cilia-like divisions), only 275-475 μ long. Cells of leaf-middle *averaging* 35-39 μ *wide* (extreme of 32 and 44 μ) x 38-44 μ long (extremes of 34 and 49 μ), rather thin-walled or slightly thick-walled, with discrete but concave-sided trigones; marginal cells near leaf-apex averaging 30-35 μ (extremes of 25 and 36 μ), with walls and trigones as in median cells, thus not forming a border, scarcely elongated parallel to margin; cells of middle of antical margin *ca.* 30-38 μ long (extremes of 25 and 46 μ) x 25-33 μ wide (extremes of 23 and 36 μ), little elongate; cells of median portion of leaf-base *ca.* 35-40 x 45-52 μ, not forming a vitta. *Median*

cells with 10-15 *oil-bodies per cell,* these mostly narrowly ellipsoidal to narrowly fusiform and varying from 3.5-4 x 9-10 μ to 4 x 11-12 μ, to a maximum of 4 x 14 μ; occasional oil-bodies short-ellipsoidal or ovate and only 3.5-4 x 5-6 μ; oil-bodies formed of mostly minute, individually protruding spherules *ca.* 1.2-1.5 μ, thus clearly, if finely, segmented; chloroplasts 2.5-3.5-4 μ in diameter; cuticle smooth. Asexual reproduction quite absent.

Sex organs unknown.

Type.—Rock Creek, above Washington, D. C. (Holzinger, 1892); isotype in NYBG examined (1952).

Distribution.—A rare and very local species, confined apparently to the Piedmont of the eastern Atlantic States.

PENNSYLVANIA: Naaman Falls in Delaware Co. (*D. Robert,* 1904; *fide* Frye and Clark, 1944, p. 442. This report is doubtful. No other students have recorded this species from so far northward. Frye and Clark also attribute the species to Virginia, citing Ammons (1940) as the authority. However, Ammons does not mention this species at all in her text). DISTRICT OF COLUMBIA: Rock Creek, above Washington, D. C., *Holzinger,* 1892 (*type;* isotype in NYBG studied). NORTH CAROLINA: Laurel Hill, New Hope Creek, Orange Co., (*Blomquist* 2721!; Duke); Eno River, W. of Christian's Mill, Durham Co., (*Blomquist* 7189!; Duke); Eno River, W. of Highway 501, ca. 4 mi. N. of Durham, Durham Co. (*Schuster and Blomquist* 28414); Laurel Hill, Eno R., NW. of Durham, Durham Co. (*Schuster and Blomquist* 28191b p.p., 28195 p.p., both with *Plagiochila asplenioides; Schuster and Blomquist* 28187, 28194, 28191a; *Schuster* 37483).

Ecology.—Reported from "boulders subject to innundation" (Evans, 1896, p. 189). In the writer's experience, the species occurs in dense shade along streams (under *Cephalanthus, Platanus, Carpinus, Betula nigra,* etc.), and may occur either on thin soil over boulders, or on soil itself, associated with *Plagiochila asplenioides, Mnium, Chiloscyphus, Scapania nemorosa, Atrichum.* The species appears to occur consistently at levels 3-6 ft. above the stream bed, at points where innundation is either rare or non-existent.

The occurence with *P. asplenioides* is particularly interesting, since this appears to be its nearest relative.

The species appears to be wholly restricted to the Piedmont with an extremely localized distribution. It is common locally along the Eno River, in the vicinity of Durham, N. C., but appears lacking elsewhere in the North Carolina Piedmont, except along the adjacent New Hope Creek. It has been searched for in a wide variety of suitable sites elsewhere, without success.

Variation.—I have seen so little material of this species that any discussion of this topic would be premature. The type material gives the impression, as does that of *P. virginica,* of being quite atypically developed. Evans (1896) describes the leaves in the type as 1600 μ long x 1100 μ wide, *i.e.,* 1.4-1.5 $\times$ as long as wide. However, this appears to be exceptional. The writer has found virtually no leaves

that are considerably longer than broad; in robust plants the leaves often average only 0.74-0.86 as long (length from insertion to the apex of the ventral lobe) as the maximal width. Even on weak shoots the leaves are no more than 1.2 as long as wide. The robust material is apparently better developed than the type. In the type material studied by the writer the leaves varied from 1.4-1.6 mm long x 1.1-1.5 mm wide, thus averaging slightly longer than wide (1.1-1.25, rarely 1.4 × as long as wide). The plants are somewhat less robust (sometimes as little as 1.7 mm wide, but usually 2-2.8 mm, occasionally to 3.6 wide). Evans (1896) describes the type as brownish or yellowish green, and the cells as thick-walled and with prominent trigones. These plants appear to represent a somewhat more xeromorphic form. As in some other species of *Plagiochila* the xeric forms (mod. *meso- vel pachyderma-parvifolia*) also tend to have narrower leaves than usual (mod. *angustifolia*). See, for instance, the notes under ***P. virginica*** var. ***caroliniana***.

In the well-developed, luxuriant material collected by the writer and Dr. H. L. Blomquist (No. 28194), at Laurel Hill, N. C., the plants are larger (mostly 3.2-4.5 mm wide), a pure green, with thin-walled cells and rather moderate, concave-sided trigones. These plants represent the mesic extreme, a mod. *viridis-lepto vel mesoderma-megafolia-latifolia.* Robust plants possess leaves that average wider than long— a condition not regularly recurring in any other regional species of the genus. In the plants of *Schuster* 37483, from the same locality, the

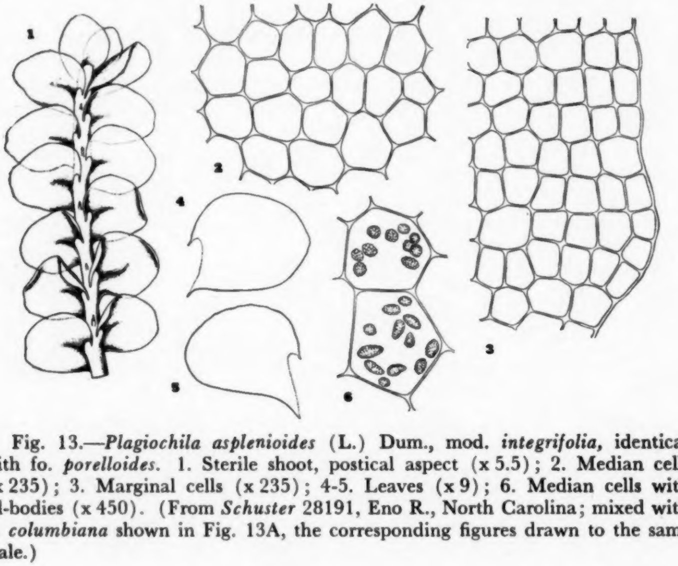

Fig. 13.—***Plagiochila asplenioides*** (L.) Dum., mod. ***integrifolia,*** identical with fo. ***porelloides***. 1. Sterile shoot, postical aspect (x 5.5); 2. Median cells (x 235); 3. Marginal cells (x 235); 4-5. Leaves (x 9); 6. Median cells with oil-bodies (x 450). (From *Schuster* 28191, Eno R., North Carolina; mixed with ***P. columbiana*** shown in Fig. 13A, the corresponding figures drawn to the same scale.)

leaves are often only 0.74-0.86 as long as wide! Attention should perhaps, in this connection, be drawn to the description of large underleaves in *P. columbiana*. Evans, *loc. cit.*, describes the underleaves as "either minute and subulate or larger, lanceolate to ovate, acute, entire or irregularly toothed or lobed. . . ." I have seen no such underleaves

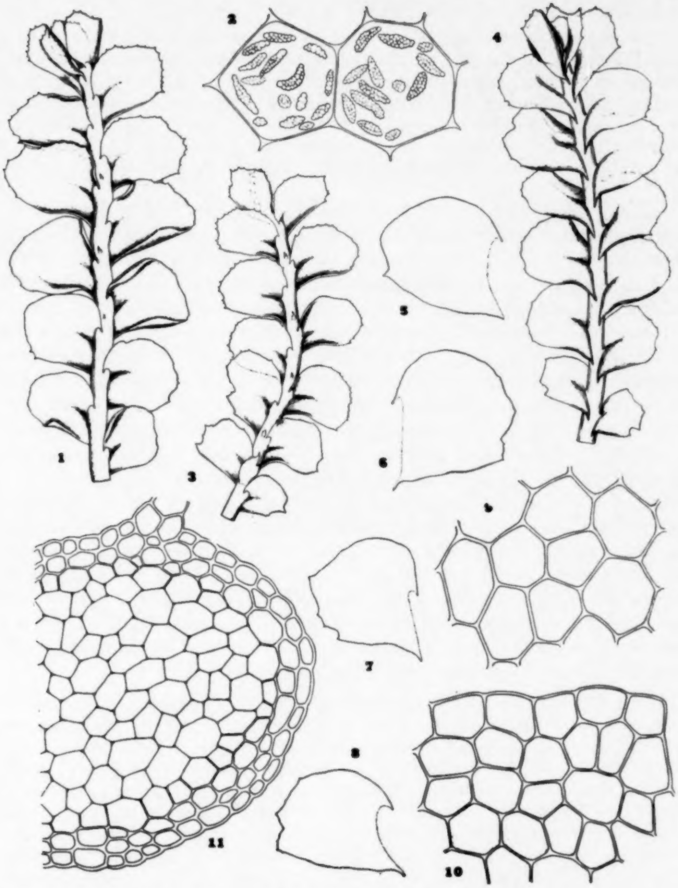

Fig. 13A.—*Plagiochila columbiana* Evs. 1,3-4. Plants of varying size (x 5.5); 2. Median cells with oil-bodies (x 450); 5. Small leaf (x 9); 6-7. Larger leaves (x 9); 8. Narrow leaf extreme (x 9); 9. Median cells (x 235); 10. Marginal cells (x 235); 11. Stem cross-section (x 120). (From *Schuster* 28191b, Eno R., North Carolina; mixed with *P. asplenioides*, in Fig. 13; corresponding figures drawn to same scale.)

in the material available to me, and can only conclude that the development of such large underleaves represents an abnormality. The only places at which lamellate underleaves have been seen are at the bases of branches, points at which all the species of the genus tend to show reversion to a nearly isophyllous condition.

Differentiation.—Evans (1896) states:

"In general appearance *P. columbiana* bears some resemblance to *P. asplenioides;* but, under the microscope, it may be distinguished at once from that species by the ragged outline of its leaves and by the irregularity in the number and position of their teeth. The latter are frequently wanting in the lower leaves and they are always few in number; as a rule they are short and blunt but they are sometimes longer and become lobe-like in character. The leaf-cells of this species are much larger than those of *P. asplenioides*. . . ."

This rare species differs considerably from our other *Plagiochilae* in the irregular dentition of the leaves, in the leaf-form, and in the large leaf-cells. The rotund-ovate leaves, with their strongly arched postical margins and slightly decurrent base, suggest forms of *P. asplenioides* (and the related *P. arctica*). However, careful study of a series of leaves shows that *P. columbiana* bears mature leaves which are shallowly 2-3-lobed, the "lobes" being exceedingly broad and vague, terminated usually by a single-celled tooth; in addition, several additional, inconspicuous 1-2-celled teeth may occur. The irregular leaf-outline, and the irregularity in the number of teeth (which never exceed 6-9 per leaf and average only 3-4 per leaf) at once separates the species from *P. asplenioides.* The species is also characterized by the relatively uniform, large leaf-cells, which are almost isodiametric (except well below the leaf-middle). The cell-width, in the leaf-middle, averages between 35-40, rarely 41 μ (in the type; I have not seen any series of cells averaging 41 μ, as Evans, 1896, indicates them to be). In the large cells, with distinct but not bulging trigones, the species differs at once from *P. asplenioides,* but resembles *P. arctica.* The marginal cells of the leaves average nearly isodiametric, and never are differentiated as a thick-walled border.

Sterile plants of *Pedinophyllum interruptum* var. *pyrenaicum* may easily be mistaken for *P. columbiana,* since the two species attain about the same size, and also have broadly ovate to ovate-orbicular leaves on robust shoots. The smaller cell-size of the *Pedinophyllum* (median cells averaging only 27-30, rarely 30-32 μ wide), as well as the minute trigones, should separate sterile plants from *Plagiochila columbiana.* The amazing resemblance in leaf-form between the two is evident from the accompanying figure of *Pedinophyllum interruptum* var. *pyrenaicum* (Spr.) Schiffn. (drawn from Schiffner's Hep. Eur. Exsic. No. 241, Basses-Pyrénées, France). Evans (1896) would separate *Pedinophyllum interruptum* from the species of *Plagiochila* on the basis of having the "Stems creeping and radiculose; leaves not decurrent"; however, he notes under *Plagiochila columbiana* "Stems . . . often sparingly radiculose," and I can find virtually no difference between the dorsally short-decurrent leaves of *Plagiochila columbiana* and the equally short-decurrent leaves of the *Pedinophyllum.*

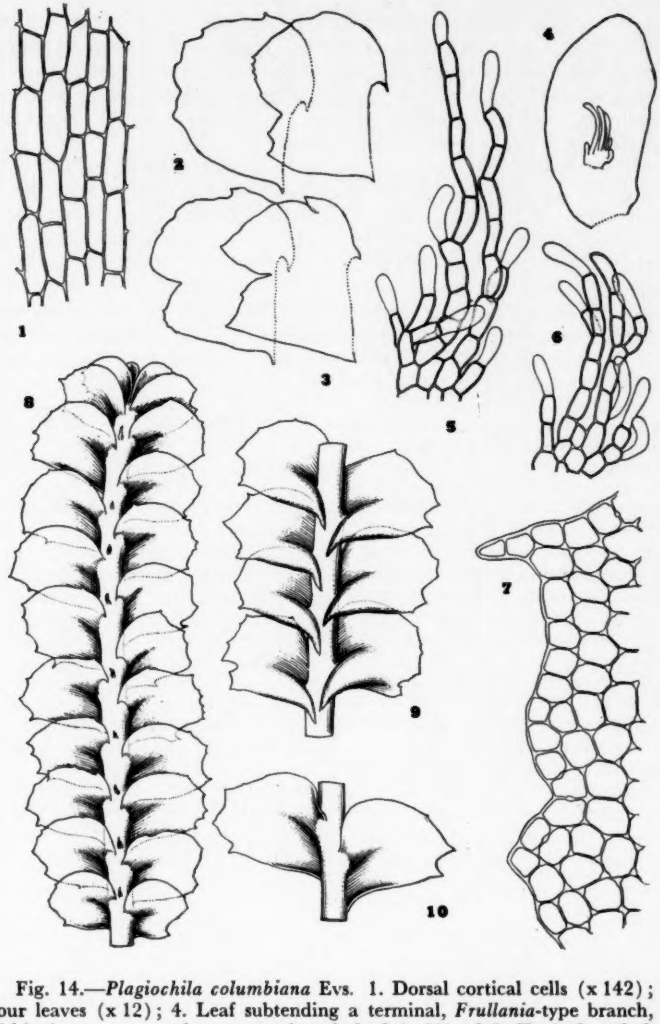

Fig. 14.—*Plagiochila columbiana* Evs. 1. Dorsal cortical cells (x 142); 2-3. Four leaves (x 12); 4. Leaf subtending a terminal, *Frullania*-type branch, and within it, to same scale, a normal underleaf (x 30); 5-6. Typical underleaves (x 120); 7. Cells of leaf apex, showing dentition of normal leaf (x 142); 8, 10. Sectors of sterile shoots, postical aspect (x 15); 9. Sector sterile shoot, antical aspect (x 13). (Figs. 1-7, from Eno R., North Carolina, *Schuster* 37483; figs. 8-10, from type specimen from Washington, D. C.)

In the final analysis, confusion of the species appears possible only with *P. asplenioides* and *arctica.* As is evident from the respective ranges, *P. columbiana* and *arctica* cannot well be identical. Furthermore, *P. arctica* has a *less quadrate* leaf-form, with the leaves rounded distally (and either quite entire or with scattered fine teeth as in the very similar *P. asplenioides*). However, *P. columbiana* and *arctica* have cells that are identical in size (see Table I), with consequent danger of confusion arising on this basis.

P. columbiana differs from *asplenioides* not only in leaf-form and larger cell-size, but also in its "behavior" and in its cytology. In the larger-celled *P. columbiana* the 10-15 oil-bodies are considerably larger, on an average (mostly 4 x 9-14 μ). In closely associated plants of *P. asplenioides,* the 9-12 oil-bodies per cell are less linear and more ellipsoidal, attain a size of from 4 x 5 μ to a maximum of 5 x 8 μ. These differences are not great, and perhaps will not prove constant, but deserve emphasis since they occurred in plants growing intermingled (and consequently under identical environmental conditions); compare Figures 13 and 13A.

As is stressed under *P. asplenioides,* juvenile plants of this species often have irregularly 2-3-lobed leaves, with occasional irregular teeth, which almost perfectly match those of *P. columbiana.* This led to the supposition that perhaps the latter represented only a juvenile form of the former. Not only the larger cells of *P. columbiana,* but the fact that the two taxa remain abundantly distinct when growing together (as in *Schuster and Blomquist* 28194) demonstrate that such a supposition is untenable. To demonstrate these differences, the accompanying figures (13 and 13A), drawn to the same scale, have been prepared of plants that had grown closely intermingled.

A final distinction between *P. columbiana* and the other species of the Sectio Asplenioides, of perhaps more theoretical than practical value, resides in the branching. *P. columbiana* does not develop a marked system of reduced-leaved creeping, prostrate rhizomatous stems; our other species are able to, and usually, if not invariably, do so. Also, *P. columbiana* is able to produce terminal branches of the *Frullania*-type, although these are rare in the few specimens seen; our other species of the section appear quite unable to produce other than intercalary branches.

Hormones Controlling the Distal Retinal Pigment of the Crayfish Orconectes clypeatus[1]

MILTON FINGERMAN, MILDRED E. LOWE, AND BANGALORE I. SUNDARARAJ

Newcomb College, Tulane University, New Orleans 18, Louisiana

Several investigators have found that the distal retinal pigment of crustaceans will move toward the fully light-adapted position after injection of extracts of eyestalks. The initial finding was made on the prawn *Palaemonetes vulgaris* by Kleinholz (1936). Welsh (1939) confirmed this observation with the crayfish *Cambarus bartoni.* Later Welsh (1941) extracted individually the components of the eyestalk of *Cambarus bartoni* and found that the sinus gland contained the most light-adapting hormone. An appreciable quantity of this substance was also present in the medulla terminalis. He found little or no active material in the supraesophageal ganglia. More recently, Brown, Hines, and Fingerman (1952) found a distal retinal pigment light-adapting hormone in the supraesophageal ganglia of *Palaemonetes.* Fingerman (1957) demonstrated the presence of this hormone in the eyestalks and supraesophageal ganglia of the dwarf crayfish, *Cambarellus shufeldti.*

Indirect evidence for a retinal pigment dark-adapting hormone in *Palaemonetes* has been presented by Brown, Hines, and Fingerman (1952). Their evidence was based on differences in rates of dark-adaptation between control prawns and those injected with extracts of various organs. However, direct evidence is lacking for a retinal pigment dark-adapting hormone, *i.e.* the demonstration of migration of the distal retinal pigment toward the fully dark-adapted position in light-adapted specimens kept under constant illumination.

The present investigation was undertaken (1) to establish by direct evidence the presence of a distal retinal pigment dark-adapting hormone in the crayfish *Orconectes clypeatus,* (2) to determine the sites in this crayfish of light- and dark-adapting hormones since regulation of the retinal pigments of this crayfish has not been studied previously, and (3) to determine if these hormones can be separated from one another by filter paper electrophoresis.

Materials and Methods

Specimens of *Orconectes clypeatus* were collected weekly at Hickory, Louisiana, for use in the experiments described below. The crayfish were kept in aquaria that contained aerated water about 2.5 cm deep.

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The method of Sandeen and Brown (1952), as modified by Fingerman (1957) for use with crayfish, was employed to facilitate rapid determination of the state of the distal retinal pigment in a group of *Orconectes*. The crayfish were placed one at a time ventral surface down on the stage of a stereoscopic dissecting microscope. With the aid of an ocular micrometer and transmitted light the following measurements were made: (1) the width of the translucent distal portion of the compound eye in a plane parallel to the long axis of the eyestalk and (2) the length of the eye from the corneal surface to the apex of the notch at the proximal portion of the eye. To render the distal clear portion of the eye more translucent and the proximal edge of the clear area more definite, the crayfish were submerged in a dish of water on the stage of the microscope. The ratio of length of clear area (measurement 1) to total length (measurement 2) is known as the distal pigment index. Use of this ratio would minimize effects of size differences. In the fully dark-adapted eye the distal pigment abutted against the cornea; the distal pigment index was 0.00. In the fully light-adapted eye the distal pigment index was about 0.10. A typical ratio for a fully light-adapted eye was 3/30.

A magnification of 60X was used in the experiments. Each unit of the ocular micrometer at this magnification was equivalent to 24.4μ. The distal pigment index of 10 crayfish could be determined with ease in three minutes. For all experiments the specimens were placed in black enameled pans with a bottom diameter of 14.5 cm. The pans contained water approximately 2.5 cm deep. These black pans were kept under a continuous illumination of 0.4 ft. c. At this intensity the distal retinal pigment was slightly less than midway toward the fully light-adapted state, the distal pigment index was about 0.04. As a result of being in this position, the distal pigment could produce either a light-adaptational or dark-adaptational response.

Specimens with one eyestalk removed were injected with tissue extracts or saline. Removal of one eyestalk results in loss of an important source of retinal pigment light-adapting hormone in all crustaceans in which endocrine control of retinal pigment migration has been investigated. Presumably, therefore, one-eyed crayfish would not be as readily able to antagonize a dark-adapting substance that might be injected as would intact specimens.

Filter paper electrophoresis of retinal pigment hormones of *Orconectes* was performed in essentially the same manner described by Fingerman and Aoto (1958) for chromatophorotropins of the dwarf crayfish, *Cambarellus shufeldti*. A model E-800-2 Filter Paper Electrophoresis Apparatus manufactured by the Research Equipment Corporation was used. The voltage was held constant at 500 volts and the current was 0.1-0.2 milliampere. When extracts were prepared, the desired number of organs (40 eyestalks or 20 supraesophageal ganglia with the circumesophageal connectives attached) was dissected out, triturated, and suspended in 0.1 ml distilled water. All extracts of eyestalks used in the experiments described below were

centrifuged after trituration to remove the bits of exoskeleton and retinal pigments. Each extract was then gradually applied to a 0.5 inch wide Whatman No. 1 filter paper strip with a cool-air blower that was used to evaporate the water as the extract was applied, thereby preventing spread of the extract over a band more than one-quarter inch wide along the paper. The entire strip was then wetted with one-tenth molar sodium borate buffer pH 7.2 and placed in the electrophoretic migration chamber. To minimize deterioration of the active substances on the paper the chamber was kept in a refrigerator maintained at an average temperature of 7°C. After electrophoresis had proceeded for two hours the filter paper strip was removed from the chamber. Three inch sections on both sides of the region of application were then sliced from the strip. The sections of the strip were not allowed to dry but instead were immediately placed into 0.3 ml Van Harreveld's solution (Van Harreveld, 1936) in covered containers to minimize evaporation. These dishes were kept in the refrigerator for 30 minutes to wash the hormones from the paper. The fluid was then collected in syringes and injected into one-eyed crayfish. The dose was always 0.02 ml per crayfish. As a control a three-inch strip of paper was wet with buffer and then placed likewise into 0.3 ml Van Harreveld's solution for 30 minutes.

Tissue extracts injected immediately after preparation into crayfish rather than after electrophoresis were routinely prepared as follows. The organs to be assayed were dissected out and placed into Van Harreveld's solution. When the desired number of each organ was available, the organs were transferred with a minimum of saline to a glass mortar, triturated, and suspended in a sufficient volume of Van Harreveld's solution to yield a concentration of one-third of a complement per 0.02 ml. Every extract was assayed on 10 specimens. Control specimens were injected with 0.02 ml Van Harreveld's solution.

Student's "t" test was used for determination of the level of significance. The 95 percent level was taken as the minimum for a significant difference between two means.

EXPERIMENTS AND RESULTS

Responses of the distal retinal pigment to freshly prepared, non-electrophoresed extracts

This series of experiments was devised to determine the effects of extracts of various tissues on the distal retinal pigment. In the first experiment extracts of whole eyestalks and their components, the sinus gland and optic ganglia, were assayed. In the second experiment the effects on the distal retinal pigment of extracts of supraesophageal ganglia plus the circumesophageal connectives, supraesophageal ganglia alone, and circumesophageal connectives alone were determined. Each experiment was performed twice. The averaged results are pre-

sented in Figure 1 where each point represents the mean of 20 specimens.

Inspection of the figure reveals that all the tissues examined contained a light-adapting substance. The degree of light-adaptation attained by the experimental crayfish at the 30-minute reading was significantly different from the controls. Within the two-hour duration of the experiment no indication of a dark-adapting hormone was apparent. With extracts of the eyestalks and the supraesophageal ganglia plus the circumesophageal connectives the light-adaptational effect caused by the whole structure was approximately equal to the sum of the effects of their components. Potency in this case may be judged by the area subtended by the curve depicting the light-adaptational response.

Electrophoretic analysis of retinal pigment hormones

The aim of the first experiment of this group was to ascertain if the eyestalk and the supraesophageal ganglia, plus the circumesophageal connectives, contain a dark-adapting hormone that could be separated from the light-adapting one by filter paper electrophoresis in the manner described above. Each tissue was used in three experiments and the results were consistent. The averaged data are presented in Figure 2 where each point represents the mean of 30 specimens.

As is apparent from inspection of Figure 2 both the eyestalks and the supraesophageal ganglia with the circumesophageal connectives attached contained a statistically significant high titer of light-adapting substance that migrated toward the cathode. A dark-adapting substance was also present and migrated toward the anode. At least a partial separation of these hormones was accomplished, the separation

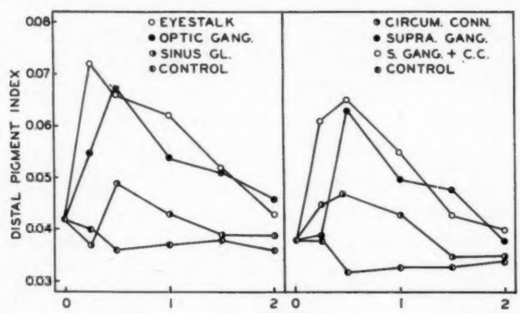

Fig. 1.—Responses of the distal retinal pigment of *Orconectes* to extracts of whole eyestalks, optic ganglia, sinus glands, supraesophageal ganglia with the circumesophageal connectives attached, supraesophageal ganglia, and circumesophageal connectives.

being more nearly complete in the case of the supraesophageal ganglia with the circumesophageal connectives attached. The curve for the dark-adapting hormone of the supraesophageal ganglia plus the circumesophageal connectives was significantly different (95 percent level) from the controls. Because of the incomplete separation of the hormones in the eyestalk the mean curve for the dark-adapting hormone of this structure was statistically different from the mean control curve only at the 80 percent level of significance. However, in view of the similarity of the results in parts A and B of Figure 2, there is no doubt that with further experimentation the 95 percent level would be reached as the number of samples becomes extremely large.

The aim of the final set of experiments was to determine the degree of antagonism between the two retinal pigment hormones in the supraesophageal ganglia with the circumesophageal connectives attached after the hormones had been separated from each other by electrophoresis. Equal volumes of extracts from the positive and negative portions of the strip were mixed. The pure extracts were diluted with an equal volume of saline to correct for their dilution in the mixture. The results are shown in Figure 3 where each point represents the mean of 20 specimens. The pure substances behaved in the manner shown in Figure 2. However, the presence of both hormones in the mixture inhibited the light-adaptational response considerably and the dark-adapting response was negligible.

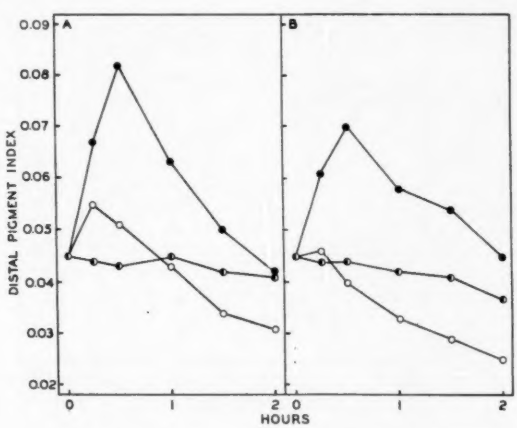

Fig. 2.—Responses of the distal retinal pigment of *Orconectes* to extracts of (A) eyestalks and (B) supraesophageal ganglia with the circumesophageal connectives attached. Filter paper electrophoresis was carried out on the extracts before injection. Circles, fraction that migrated toward the positive pole; dots, fraction that migrated toward the negative pole; half-filled circles, control.

DISCUSSION

The experiments described above provide the first direct evidence for a distal retinal pigment dark-adapting hormone in crayfishes. Conceivably, with further investigation antagonistic light-adapting and dark-adapting hormones will be found in other species. A similar situation prevailed several years ago in studies of chromatophores. In most crustaceans the early investigators found either a pigment-dispersing or concentrating hormone alone. With refined techniques both substances have been demonstrated in many species. For example, the red chromatophores of *Orconectes clypeatus* are controlled by lightening and darkening substances (Fingerman, 1958). Eventually all functions mediated by hormones in crustaceans may be shown to be controlled by antagonistically functioning substances.

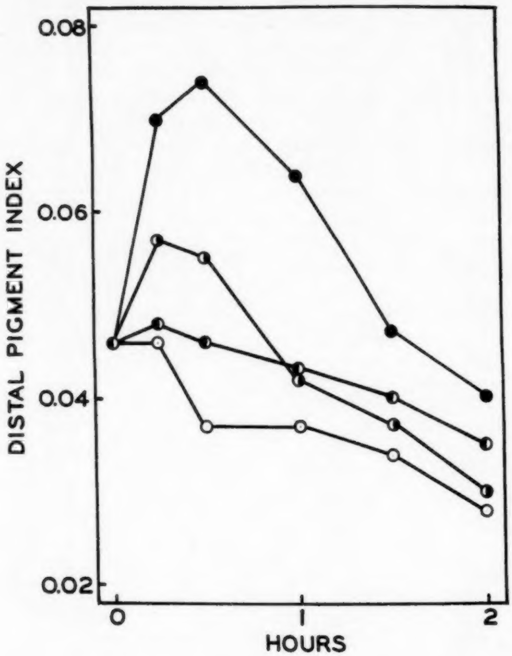

Fig. 3.—Responses of the distal retinal pigment of *Orconectes* to extracts of the supraesophageal ganglia with the circumesophageal connectives attached after filter paper electrophoresis. Circles, positive portion of the strip; dots, negative portion of the strip; circles half-filled on left, control; circles half-filled on right, mixture of equal volumes of the fractions from the positive and negative parts of the strip.

Welsh (1939) reported that the eyestalk of *Cambarus bartoni* contained a retinal pigment light-adapting hormone. This observation has been verified now for two other crayfishes, *Cambarellus shufeldti* by Fingerman (1957) and *Orconectes clypeatus* herein. In 1941 Welsh reported that he was unable to detect any significant quantity of light-adapting hormone in the supraesophageal ganglia of *Cambarus bartoni*. However, the supraesophageal ganglia of *Orconectes clypeatus*, (Figure 1B) and *Cambarellus shufeldti* (Fingerman, 1957) contain appreciable quantities of light-adapting material. Such differences among species of crayfishes indicate that it is hazardous to assume *a priori* that all crayfishes will fall into one pattern.

SUMMARY AND CONCLUSIONS

Direct evidence is provided for distal retinal pigment dark-adapting and light-adapting hormones in the crayfish *Orconectes clypeatus*.

These substances can be separated from one another by filter paper electrophoresis. At pH 7.2 the light-adapting substance is electropositive and the dark-adapting one electronegative.

The results were discussed in relation to the information available concerning the endocrine control of retinal pigments in other crayfishes.

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The Ants of Bidwell Park, Chico, California[1]

ADRIAN M. WENNER[2]
Chico State College, Chico, California

The ant fauna of northern California is poorly known. Although Mallis (1941) has published an annotated list of the species of ants found in California and Cook (1953) has surveyed the literature on the ants of California, locality records and notes on the life histories of northern California ant species are very few (i.e. of the localities mentioned in Mallis' work, less than 8 percent are in the Sacramento River drainage system, an area which includes about one-fourth of the area of the state; none of the localities is in the upper Sacramento Valley).

The Bidwell Park area is interesting for the study of ants in that it has a diversity of flora and habitats which is representative of a great portion of the Sacramento Valley and surrounding foothills. Athough it is not an entirely natural area, being changed continually by grazing, pruning, and introductions, it is a relatively permanent unit in which individual sections have remained unchanged for many years.

Material for this paper was collected, and observations were made, within the park, throughout the Sacramento Valley, and in the surrounding foothills between December, 1953 and June, 1956. Unless otherwise noted in the accounts to follow, all species which are mentioned were collected in the park. The localities listed at the end of each account represent additional records in habitats similar to that found in the park. Locations of these stations in air miles from the Chico State College campus are as follows: Centerville, 8 mi. E; Fair Oaks, 82 mi. S; Glenn, 19 mi. SW; Hamilton City, 10 mi. W; Lakehead, 105 mi. N; Live Oak (Sutter Buttes), 31 mi. S; Modoc County, 147 mi. NE; Mt. Shasta City, 113 mi. N; Orland (Newville,), 30 mi. W; Oroville, 21 mi. SE; Paradise, 13 mi. E; Paynescreek, 42 mi. N; Paskenta, 40 mi. W; Willows, 23 mi. SW.

Acknowledgment—I am indebted to Dr. Homer J. Lowe for his guidance and supervision and to Drs. Margery Anthony, Fred Neumann and Gerald Scherba, all of Chico State College for their advice and help. The identity of the specimens herein described was verified by Dr. Marion R. Smith of the U. S. Department of Agriculture.

Description of Area

Bidwell Park, included within the boundaries of Chico, Butte County, lies on the eastern edge of the northern Sacramento Valley.

[1] This paper is part of a thesis submitted in partial fulfillment for the Master of Arts degree, Chico State College.

[2] Present address: Department of Zoology; University of Michigan; Ann Arbor, Michigan.

Half its linear length extends into the valley; the other half reaches into the foothills of the Cascade-Sierra Nevada Range (Fig. 1).

During the Miocene, approximately twenty million years ago, volcanic action in this area covered the Cretaceous ocean deposits with a layer of basalt. From a period of about four million to one million years ago, (late Pliocene) this was covered repeatedly with ash and mudflows to a considerable depth; these deposits subsequently became conglomerate and breccia. Recent uplifting in the mountains to the east resulted in a tilted lava plateau which extends under the present valley floor, about four hundred feet beneath the central part of Chico.

Chico Creek, flowing in a southwesterly direction to join the Sacramento River, cut into the plateau greatly as it tilted, forming an alluvial fan upon which the city of Chico now rests. In cutting into the plateau it has formed Iron Canyon, and in the upper reaches of Bidwell Park it has Cretaceous deposits.

At the lower park elevations, two hundred feet, there are two major plant communities; a valley oak (*Quercus lobata* Neé) community and a cottonwood-sycamore, streamside community. Along the stream the dominant trees are western sycamore (*Platanus racemosa* Nutt.), cottonwood (*Populus fremontii* Wats.), and alder (*Alnus rhombifolia* Nutt.); wild grape (*Vitis californica* Benth.), blue elderberry (*Sambucus glauca* Nutt.) and willow (*Salix* sp.) are common. Blackberry (*Rubus vitifolius* C. & S.), western redbud (*Cercis occidentalis* Torr.), and spicebush (*Calycanthus occidentalis* H. & A.)

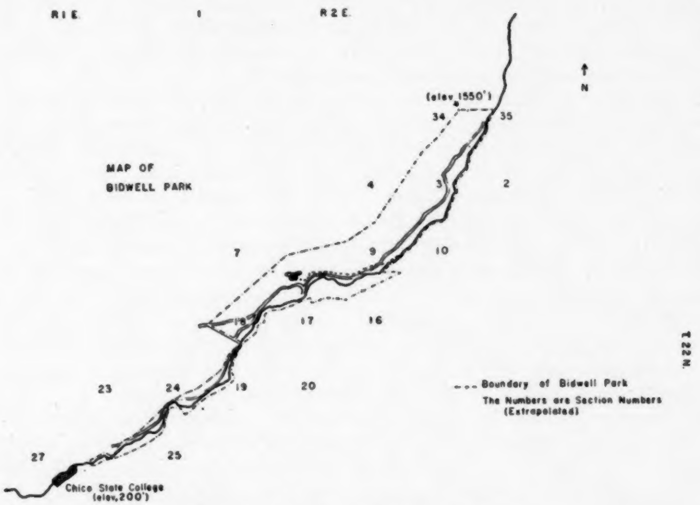

Fig. 1—The Bidwell Park study area.

are also found. Blue gum (*Eucalyptus* sp.) occurs away from the stream in the valley oak community.

At the upper end of the alluvial fan, at an elevation of three hundred feet, just before the stream emerges from the canyon, the vegetation forms a typical foothill community, with blue oak (*Quercus douglasii* H. & A.), live oak (*Q. wislizenii* A. DC.), and digger pine (*Pinus sabiniana* Dougl.) as dominants, and wedgebeat buckbrush (*Ceanothus cuneatus* Nutt.), manzanita (*Arctostaphylos manzanita* Parry), poison oak (*Rhus diversiloba* T. & G.), California buckeye (*Aesculus californica* Nutt.), mountain balm (*Eriodictyon californicum* H. & A.), mule fat (*Baccharis viminea* D. C.), and toyon (*Photinia arbutifolia* Lindl.) also present as typical members of this community.

DISTRIBUTION OF ANTS

In and among the cottonwoods, sycamores, and all species of oaks, *Liometopum occidentalis* Emery was found to be the dominant species. *Prenolepis imparis* Wheeler, *Camponotus* (*Myrmentoma*) sp. and *Camponotus maccooki* Forel were found at the base and in the oaks.

Tapinoma sessile Say was the species occupying the greatest variety of habitats in the park; it was found under objects or in mulch either near or away from trees.

Veromessor andrei Mayr was found on the alluvial wash near oaks and was not found in open grassland in the park area. In the latter habitat, *Veromessor stoddardi chicoensis* Smith prevailed, together with *Pheidole californica* Emery. *Pheidole hyatti* Emery occupied an area similar to that of *V. andrei* or *P. californica*. The habitat of *Formica rufibarbis occidua* Wheeler was nearly coincident with that of *V. andrei* and *L. occidentalis* combined.

Formica lasioides Emery, *Lasius niger neoniger* Emery, *Monomorium minimum* Buckley, *Solenopsis molesta* Emery, *Ponera trigona opacior* Forel, and *Aphaenogaster subterranea occidentalis* Emery have been found on the border of or in moist locations.

Formica sanguinea subnuda Emery and *Dorymyrmex pyramicus* Roger were found in similar habitats, open areas in the shade of valley oak trees. However, outside the park, *D. pyramicus* was found in unshaded areas. Nests of *F. sanguinea* were found in short, sparse grass, and *D. pyramicus* nests were found on bare plots of earth.

In the city adjacent to the park, the Argentine ant (*Iridomyrmex humilis* Mayr) was extending its range. *Solenopsis xyloni* McCook infested lawns and sidewalks in sunny areas, and *Formica altipetens* Wheeler was readily found near sidewalks on clear days.

Formica integroides Emery, *Camponotus vicinus* Mayr, *Crematogaster* sp. and *Pogonomyrmex subdentatus* Mayr are mentioned in this paper since they were found at elevations and in habitats similar to those present in the park. A more careful search with the use of better collecting methods (Headley, 1952) would probably establish

that the above three species, as well as several others, were present in the park area.

ACCOUNTS OF SPECIES

The taxonomic treatment follows that of Creighton (1950). Representative specimens are deposited in the collections of the Department of Biology, Chico State College, Chico, California.

PONERINAE

Ponera trigona opacior Forel—Although this species was not found in the defined area of the paper, two records are present from adjacent territories. Fourteen workers were dug from a clay-loam bank at the lower end of the chaparral belt, and one dealated female was found under a small rock at the bottom of a draw approximately one mile south of Big Chico Creek.

Localities:—Chico, 300 feet; Paradise, 1000 feet.

MYRMICINAE

Pogonomyrmex subdentatus Mayr—One relatively small colony was found in the bottom of a draw in the foothills on the western side of the Sacramento Valley at an elevation similar to that found in Bidwell Park, but in a region much more arid than on this eastern side of the valley. The nest was in cobblestone wash without a crater or mound in evidence. In Fair Oaks, the nest was on flat open ground and inconspicuous. Some ants were observed foraging in late March and late April: examination of a chamber in the nest disclosed aphids, flies, spiders, and seeds.

Several colonies which may represent a different taxon than *P. subdentatus* were found on Table Mountain near the road which leads from Oroville and which runs across the flat top of the mountain. These nests were conspicuous; the vegetation was cleared away and gravel from the excavation was distributed near the entrance. These ants attacked readily, while individuals of *P. subdentatus* did not.

This genus may occur on flat open grassland at higher elevations within the described area of Bidwell Park.

Localities:—Orland (Newville), 830 feet; Fair Oaks, 75 feet; Oroville (?).

Aphaenogaster subterranea occidentalis Emery—This relatively slender, slightly polymorphic ant is common in moist, shady locations. Nests were found under rocks, under a board, at the base of a tree in wet leaves, and, in one case, in a bank of earth with its galleries intermingled with those of *Camponotus maccooki.* Nests were found every month of the year, but no above-ground activity was observed until mid-April. Seeds were found in a nest chamber approximately 1 cm in diameter during the first part of April.

Localities:—Glenn, 170 feet; Chico, 200 feet; Lakehead, 1000 feet; Chico (Centerville), 560 feet.

Veromessor andrei Mayr—In all but one instance this common ant was found just above the canyon bottom on flat, open ground near trees. The nests may be under, or at the sides of large rocks, but a large amount of chaff obscures the use of rocks by the ants. Early in April, separate craters of earth are present around the holes of the nest. By May, these craters are combined into a low mound topped with a great amount of chaff. Under this packed chaff, larvae may be seen through the entrance holes. When the chaff layer was broken, the ants came out to attack, but did not directly protect the larvae. No activity occurs in the summer during the heat of the day; however, in late evening and early morning the ants may be seen in long loose files, carrying seeds and bits of insects. One observed file was over seventy feet long. Observations at night (12 p.m. and 2 a.m.) in October revealed activity as great as has ever been observed during the day by this author. Males were seen flying from the nest at 7 a.m. in October. While day time activity appears to be greatest in spring and fall, ants have been found above ground every month of the year. An ant cricket (probably *Myrmecophila oregonensis* Bruner) was often seen travelling in and out of the entrance in late evening and at night.

Localities:—Chico, 250 feet; Paskenta; Fair Oaks, 75 feet; Chico (Centerville), 560 feet.

Veromessor stoddardi chicoensis Smith—The nest of this species was found on open ground away from trees, occasionally under rocks. Close files sometimes over 50 feet long, were observed leading away from the nest. The files lay within a pathway in the grass and led from the nest in only one direction at any given time. The beginning of columns were seen at about 8 a.m. and at about 8 p.m. More complete notes on the life history of this species have been published by Smith (1956).

Localities:—Chico, 250 feet; Live Oak (Sutter Buttes).

Pheidole californica Emery—Larvae of this species were found in the nests on the first of March, while eggs and callow workers were found in November. Workers also foraged at night as late as November. Nests were found from the top of the lava plateau to the bottom of the canyon and into the middle of the valley. In Bidwell Park, small rocks partially enclosed by growths of club moss (*Selaginella* sp.) yielded colonies which contained plant seeds, insects and parts of insects, together with megasporangia and microsporangia of *Selaginella*. Nests have also been found under tin and under boards. Where no objects conceal the entrance, a crater of sand is initially formed around a circular entrance. Later, only dispersed material marks the entrance.

Localities:—Lakehead, 1000 feet; Chico, 200-1500 feet; Paskenta; Glenn (Ord Bend), 170 feet.

Pheidole hyatti Emery—This species was found south of Chico on

the live oak-grassland lava plateau and on the valley oak-grassland of the park. At the former location the nest was under a rock near a fencepost in the bottom of a draw. At the latter location its habitat was similar to *V. andrei.* Seeds of annual plants were found in the nests.

Localities:—Chico, 25- feet; 350 feet.

Crematogaster sp.—In late November individuals were observed feeding on honey in a warehouse; west of Willows they carried seeds of burr clover into the nest. In May, individuals were seen feeding on dead bees.

Localities:—Glenn (Ord Bend), 170 feet; Willows.

Monomorium minimum Buckley— Only one nest was found; it occurred on bare ground near brush. A crater of fine sand surrounded the entrance. Foraging for bits of insects and small seeds is done individually.

Localities:—Chico, 200 feet; Mt. Shasta City, 3700 feet.

Solenopsis xyloni McCook—This highly polymorphic ant, noted for its sting, was common near dwellings, but was not found in Bidwell Park. During the winter of 1955-56 this species was frequently observed in houses feeding on grease and waste material lodged in cracks near the sink. The nests, located in sunny areas, usually have many openings which follow some natural or artificial lines (i.e. cracks in the earth or sidewalk edges). Warm days during January prompt activity, and craters about each nest entrance become evident in vacant lots. Activity is widespread toward the end of February and the many regular craters become merged into a scattered network of shallow sand piles. Activity may be observed during every month of the year, especially during warm, clear days. Flights of winged forms were recorded on the first of June and in mid-July.

Localities:—Chico, 200 feet.

Solenopsis molesta validiuscula Emery—A digger pine nut, unearthed from approximately an inch below the surface, yielded thirteen workers and some eggs in October, 1953. Subsequently, additional nests were found, in no case with an outside entrance evident. A chamber of one nest, about 4 inches below the surface in fine sandy soil, contained a queen, brood, and workers. Its channels intermingled with those of *Lasius niger neoniger.* In another nest of *S. molesta* channels were observed intermingled with those of *Formica rufibarbis occidua.* These records of *S. molesta* nests in close proximity to the nests of other species are in accord with similar observations discussed by Mallis (1941: 12). He found individuals of this species in nests of *Tapinoma sessile* Say, *Camponotus sansobeanus maccooki* Forel, and *Prenolepis imparis* Say (probably var. *californica* Wheeler), as well as in their own independent nests. Nests were found under rocks well-isolated from any other species and, in eastern Oregon, one small rocky

knoll was a complex network of a nest or nests of this species. Three of these yellow monomorphic ants were seen attacking one *Aphaenogaster subterranea occidentalis* worker. They have been noted in kitchens feeding on grease. A chamber in one nest contained minute seeds.

Localities:—Chico, 200 feet; Glenn (Ord Bend, 170 feet; Paradise, 1000 feet.

DOLICHODERINAE

Liometopum occidentale Emery—This is the most abundant ant in the vicinity of Chico. Activity occurs during all months of the year and over a wide temperature range. Nests are found in cavities at the bases of cottonwood, sycamore, and oak trees. The ants attack readily, feed upon tree sap, and tend English ivy aphids. A male was observed at the end of March, and a flight of winged forms was observed on the tenth of December.

Localities:—Chico, 200 feet; Lakehead, 1000 feet; Paskenta.

Iridomyrmex humilis Mayr—The well-known Argentine ant has not yet been found within Bidwell Park, but as of January, 1956 was found a fraction of a mile away. Although they nest in buildings, at the base of trees, and under objects, several nests were craterless holes leading down from the surface of bare earth. In no case was a simple nest found; the pattern of nests is that of a series of chambers connected by long, closeknit files. This ant is active throughout the year and is a household pest.

Localities:—Chico, 200 feet; Hamilton City, 175 feet.

Dorymyrmex pyramicus Roger—Individual foraging occurs from April through November. Color varies from nest to nest, but is uniform within each nest. The regular craters, built on bare, shady ground, first appear about the middle of April.

Localities:—Chico, 200 feet.

Tapinoma sessile Say—This species is probably the most prominent ant in the defined area. Active foraging was observed from the first of March to the end of November. Nests occur in all habitats; the ants use almost any available cavity for nest locations.

Localities:—Chico, 200 feet; Glenn, 175 feet; Oroville; Paskenta; Orland (Newville), 830 feet; Mt. Shasta City, 3700 feet; Lakehead, 1000 feet.

FORMICINAE

Camponotus (*T.*) *maccooki* Forel—Nests of this large ant are common in the Chico vicinity. Consistent failure to see much daytime activity and observation of extensive nighttime foraging for insects in oaks indicates that the species is primarily nocturnal. Many records were obtained by excavating just underneath the symmetrical 6-7 inch

craters of rolled nodules of earth. The entrance in the center of the circular craters of these ants leads to horizontal channels 4-6 inches below the surface. These craters appear at the end of February. During mid-April well-developed larvae may be uncovered. One dealated female was found on the surface of the ground at midnight near the end of October. Accidental exposure of the interior of a nest in an earthen bank on the southern slope of a canyon disclosed a chamber two-inches in diameter with seed husks on its floor. An ant cricket (probably *Myrmecophila oregonensis* Bruner) was found in the same chamber. In one nest excavation, the channels of *Aphaenogaster subterranea occidentalis* intermingled with those of *C. maccooki.* The nests are usually found near brush or trees, and occasionally under rocks or logs.

Localities:—Chico (Centerville), 560 feet; Glenn, 170 feet; Lakehead, 1000 feet; Chico, 300 feet; Modoc Co.

Camponotus (T.) vicinus Mayr—The carpenter ant was not collected within the limits of the park. At higher elevations it is common and is locally called the "big mountain ant." Nests are found in wood either dead trees, stumps, or old frame houses.

Localities:—Paradise (Magalia), 2000 feet; Lakehead, 1000 feet; Mt. Shasta City, 3700 feet.

Camponotus (Myrmentoma) sp.—A single nest was found in the wall of a honey warehouse. A file led from a window casement, across the glass, to the tip of a branch, and on through the shrubbery to the other side of a drainage ditch. More often, widely scatter files were found on the trunks of oak trees, but records of activity on the ground were also collected. Five workers were collected inside an oak gall (valley oak) and one ant was seen going into an uprooted cottonwood stump on the bank of Chico Creek. Aside from observations of feeding on honey, little is known of the feeding habits of this species.

Localities:—Chico, 200 feet, 300 feet; Glenn (Ord Bend), 170 feet.

Prenolepis imparis californica Wheeler—This ant frequently occurs on the trunks of trees or on foliage, especially on plants with exuding sap or nectaries. In one house they were pests, nesting under the hearth and foraging in the kitchen. Dealated females were seen in files leading up a tree trunk during late March, and two males were collected by sweeping four days later. All the nests found outside of buildings were in rich mulch at the base of trees.

Localities:—Chico, 200 feet; Lakehead, 1000 feet; Paynescreek; Paradise, 2000 feet, Paskenta.

Lasius niger neoniger Emery—The craters of fine sand made by this ant were first noticed in early April on a shady bare area on the creek bank. Horizontal channels approximately 1 cm below the surface and lower chambers were unearthed. Green aphids were found

in the nest. Channels of *S. molesta* were observed intermingled with those of *L. niger*.

Localities:—Chico, 200 feet; Glenn (Ord Bend), 170 feet; Hamilton City, 175 feet.

Formica lasioides Emery—This species was observed with its nest under the same rock as the nests of *F. altipetens*. No fighting was seen when individuals of both species met. Other nests were found under rocks, sidewalks, or in the open. Nests in the open had a single entrance surrounded by a sand crater.

Localities:—Chico, 200 feet.

Formica sanguinea subnuda Emery—An inconspicuous nest occurred about 30 feet from the creek in dry, mowed grass. Scattered debris surrounded the several holes which led into the nest. Individual foraging for dead insects was observed in tall, dry grass near the creek.

Localities:—Chico, 200 feet; Live Oak (Sutter Buttes).

Formica altipetens Wheeler—Sand, irregularly scattered about the entrance, marks the location of the nest of this species. Nests occur under rocks or sidewalks. A nest was collected under the same rock as a nest of *F. lasioides*.

Localities:—Chico, 200 feet.

Formica rufibarbis occidua Wheeler—As a result of nest disturbance, this species deserts its eggs and larvae. The nest is unmarked and usually consists of a hole, near brush or trees, leading downward into the ground or under a rock. The nests are sometimes located under or in wood. Activity begins during early March, and by mid-April pupae may be observed in the nest.

Localities:—Chico 250 feet; Chico (Centerville) 560 feet.

Formica integroides Emery—This ant was not collected in or near Bidwell Park, but at a comparable elevation near Shasta Dam, which might indicate a possible occurrence at higher elevations in the park. Its nest is marked by a thatched mound, covering, or partly covering, a log or stump, and is the only nest with such an appearance in this region.

Localities:—Lakehead, 1000 feet; Mt. Shasta City, 3700 feet.

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Plants of Winter Island, N.W.T.

MAXIMILIAN G. DUMAN

Catholic University of America, Washington, D. C.

Winter Island lies off the southeast coast of Melville Peninsula near Lyon Inlet in southern Foxe Basin. On August 27, 1938, Rev. Artheme Dutilly and the author visited this island, and in a few hours collected 98 species of plants. Due to adverse ice conditions the Eskimo mission supply ship, Therese, on which we were travelling through the generosity of the Oblates of Mary Immaculate, was forced to seek shelter in a small bay on the east side of Fisher Point (66°08'N.; 83°03'W.). Taking advantage of this delay we spent about five hours botanizing on the southeastern end of the island.

The eastern side of Fisher Point which is about 76 feet high, is quite steep except for the gravel shore of one small bay. Inland the land is low and marshy with several small lakes. In this area plant growth was abundant.

Parry's Second Arctic Expedition

Winter Island is famous as the winter quarters of Parry's second arctic expedition. His ships, Fury and Hecla, arrived in the bay on the western side of Fisher Point on October 6, 1821, after much difficulty due to ice conditions. It was July 2, 1822, before they finally were able to sail out of the bay, and then only after lanes were cut in the ice through which the ships passed to open water.

Hooker (1825) reported 214 species of plants collected by Parry and his officers during this expedition. Only seven of these, four flowering plants and three lichens, are cited as collected on Winter Island. Evidently Hooker did not see all the specimens collected, as Polunin (1940) cited ten species of flowering plants collected by the members of this expedition on Winter Island.

When we consider the severe weather conditions during their stay on this isolated island we can understand the small number of species collected. Winter had already set in when they arrived, and Parry's (1824) narrative gives us some idea of the late spring. On April 12 they began clearing away snow for a garden. A few days later the frames were ready and "sown with mustard, cress and pease." The project was somewhat premature, for a month later they were still melting snow for the garden as the only source of water. On May 17 "A great deal of snow fell . . . and our unfortunate gardens were once more buried beneath it." On May 21 the narrative continues, "Not a single (native) plant was found in the state of vegetation," and on May 31, "Vegetation seemed labouring to commence, and a few tuffs of the saxifraga oppositifolia, when closely examined, discovered some sign of life." On June 9 Parry continued, "The first flower of

the saxifraga oppositifolia was brought on board as a matter of curiosity by our botanists." Finally on June 29, four days before leaving the island, he observed, "The vegetation had also felt the good effects of the late mild and moist weather, and a number of plants were now appearing in flower. Among these, specimens of the potentilla nivea, saxifraga caespitosa, draba alpina, and oxytropis arctica had been procured within the last three or four days."

Fifth Thule Expedition

Winter Island was also visited by members of the Fifth Thule Expedition. Peter Freuchen collected two Eider Ducks there on July 18, 1922, and observed another on February 20, 1923 (Hoerring, 1937), but evidently no plants were collected (Groentved, 1937; Hesselbo, 1937; Lynge, 1937).

Bartlett-Norcross Expedition

An expedition led by Captain Robert Bartlett visited Winter Island in 1933 and restored the graves left by Parry's expedition (Bartlett-Norcross, 1934). Polunin (1940) cited only one species (*Stellaria longipes* Goldie; Angel 85) collected on Winter Island by this expedition.

List of Plants

The writer is grateful to the following specialists for identifying critical species: B. Lynge, W. C. Steere, C. R. Ball, J. R. Swallen, F. J. Herman, H. O'Neill and E. Lepage.

Collection numbers in the 2200 range are the author's; those in the 6900 range are A. Dutilly's. Some of these plants have been included in other papers: Lichens by Lynge (1939), Bryophytes by Steere (1941), Carices by Duman (1941) and Calder (1951). The other collections are previously unreported.

Those species which are not marked on Porsild's (1957) range maps as occurring on Melville Peninsula north of Repulse Bay are indicated by asterisks.

Thallophyta

ALGAE

NOSTOCACEAE

Nostoc commune Vauch. 6948.

RIVULARIACEAE

Rivularia biasolettiana Menegh. 6944a.

ULVACEAE

Enteromorpha micrococca Kuetz. 6943.

LICHENES

PANNARIACEAE

Psoroma hypnorum (Vahl.) Gray. 6941.

LECIDEACEAE
Lecidea limosa Ach. 6941.

CLADONIACEAE
Cladonia lepidota var. *stricta* (Nyl.) DR. 6940.
C. pyxidata var. *neglecta* (Flk.) Mass. 2245, 6941.

LECANORACEAE
Ochrolechia frigida (Sw.) Lynge. 6941.

PARMELIACEAE
Cetraria nivalis (L.) Ach. 2242, 6942.
C. cucullata (Bell.) Ach. 2242a, 6942a.
C. tilesii Ach. 2242b, 6942b.

USNEACEAE
Dactylina ramulosa (Hook.) Tayl. 6942c.

CALOPLACACEAE
Caloplaca subolicacea (Th. Fr.) Lynge. 6942d.
C. elegans (Link) Th. Fr. 2250, 6947.

PHYSCIACEAE
Physcia caesia (Hoffm.) Hampe. 6947a.

LICHENES IMPERFECTI
Thamnolia vermicularis (Sw.) Ach. 2242c, 6946.

Bryophyta

DITRICHACEAE
Distichium capillaceum (Hedw.) Bry. eur. 6934f.
Ditrichum flexicaule (Schwaegr.) Hampe. 2235c, 6934m.

POTTIACEAE
Didymodon rufus Lor. 6934j.
Tortula ruralis (Hedw.) Smith. 2235b, 6934k.

CATOSCOPIACEAE
Catoscopium nigritum (Hedw.) Brid. 2236, 6934d.

TIMMIACEAE
Timmia austriaca Hedw. 6934g.

AMBLYSTEGIACEAE
Amblystegium serpens (Hedw.) Bry. eur. 6934n.
Campylium protensum (Brid.) Lindb. 6935c.
C. stellatum (Hedw.) Lange and Jens. 2234b.
C. polygamum (Bry. eur.) Bryhn. 2233.
Drepanocladus fluitans (Hedw.) Warnst. 2240a.
D. exannulatus (Guemb.) Warnst. 6936.
D. revolvens (Muell.) Warnst. 2234a, 6934c.
D. sendtneri (Schimp.) Warnst. 6935a.
D. uncinatus (Hedw.) Warnst. 2233a, 6934e.
Calliergon turgescens (Schimp.) Lindb. 6935b.

BRACHYTHECIACEAE

Tomenthypnum nitens (Hedw.) Loeske. 2237a, 6934i.
Cirriphyllum cirrhosum (Schwaegr.) Grout. 6934l.
Brachythecium salebrosum (Hoffm.) Bry. eur. 6934h.
B. albicans (Hedw.) Bry. eur. 2233b.

ENTODONTACEAE

Orthothecium strictum Lor. 6934b.

HYPNACEAE

Hypnum cupressiforme Hedw. 6934a.
H. revolutum (Mitt.) Lindb. 2235a.

Pteridophyta

EQUISETACEAE

Equisetum variegatum Schleich. 6938.

Spermatophyta

GRAMINEAE

Hierochloe pauciflora R. Br. 2275, 6971a.
**Alopecurus alpinus* L. 2255, 6956.
Phippsia algida (Sol.) R. Br. 2256, 6955.
Arctagrostis latifolia (R. Br.) Griseb. 2271, 6960.
**Deschampsia caespitosa* (L.) Beauv. 2252.
**Trisetum spicatum* var. *maidenii* (Gand.) Fernald. 2259, 6957.
**Poa alpigena* var. *colpodea* (Fr.) Schol. 2277.
**P. arctica* R. Br. 2258, 6926.
P. glauca Vahl. 2273, 6971.
Dupontia fisheri R. Br. 2261, 6968a.
Puccinellia vahliana (Liebm.) Schribn. and Merr. (*Colpodium vahlianum* (Liebm.) Nevski.) 6959.
**P. paupercula* (Holm) Fern. and Weath. (*P. langeana* (Berl.) Soerensen). 2260, 6951.
**P. phryganodes* (Trin.) Scribn. and Merr. 6979c.
Festuca brachyphylla Schultes 2280, 6973.

CYPERACEAE

**Eriophorum angustifolium* Honck. 2267, 6966.
E. scheuchzeri Hoppe. 2267a, 6967.
Carex nardina Fr. 2287, 6979a.
C. ursina Dew. 2254, 6978.
**C. maritima* Gunn. (var. *setina* (Christ) Fernald). 2268, 6979b.
C. bipartita Bellardi ex All. 6980r.
C. glareosa var. *amphigena* Fernald. 2251, 6950.
C. stans Drej. 2284, 6978.
**C. rariflora* (Wahl.) Sm. 6980n.
C. vaginata Tausch. 6981e.
C. misandra R. Br. 2278, 6976.
**C. capillaris* L. 6905.
**C. membranacea* Hook. 2283, 6977.

JUNCACEAE

Juncus biglumis L. 2265, 6964.
Luzula confusa, Lindebl. 2262, 6961.

SALICACEAE

Salix reticulata L. 2225, 6924.

S. anglorum Cham. (*S. arctica* Pall.). 2223, 6922.—Porsild and others consider *S. anglorum* an eastern species. Ball, who identified these specimens, also named 6923 var. *antiplasta* Schneider, and 6922b var. *kophophylla* Schneider.

POLYGONACEAE

Oxyria dignya (L.) Hill. 2227, 6928.

Polygonum viviparum L. 2208, 6907.

CARYOPHYLLACEAE

Stellaria longipes Goldie. 2215, 6915.

Cerastium alpinum L. 2216, 6916.

**Arenaria peploides* var. *diffusa* Hornem. 2205, 6902.

**Lychnis apetala* var. *arctica* (Fr.) Cody. 2201, 6903.

RANUNCULACEAE

Ranunculus hyperboreus Rottb. 2238, 6933.

PAPAVERACEAE

Papaver radicatum Rottb. 2232, 6933.

CRUCIFERAE

**Cochlearia officinalis* ssp. *arctica* (Schlecht.) Hulten. 2210, 6910.

Eutrema edwardsii R. Br. 2211, 6911.

Cardamine pratensis var. *angustifolia* Hook. 2214, 6914.

**Draba bellii* Holm. (*D. alpina* var. *nana* Hook.) 2213, 6913.

SAXIFRAGACEAE

**Saxifraga caespitosa* ssp. *uniflora* (R. Br.) Porsild. 2230, 6930.

S. cernua L. 2228, 6926.

S. oppositifolia L. 2231, 6931.

S. tricuspidata Rottb. 2229, 6929.

ROSACEAE

Potentilla hyparctica Malte. 2209, 6908.

Dryas integrifolia Vahl. 2217, 6917a.

LEGUMINOSAE

Astragulus alpinus L. 2218, 6920.

Oxytropis maydelliana Trautv. 2220, 6919.

O. arctobia Bunge. 2226, 6925.

ONAGRACEAE

Epilobium latifolium L. 2207, 6906.

ERICACEAE

Cassiope tetragona (L.) Don. 2222, 6921.

SCROPHULARIACEAE

Pedicularis hirsuta L. 2204, 6904.

COMPOSITAE

Erigeron unalaschkensis (DC.) Vierh. 2200, 6900.

Chrysanthemum integrifolium Richards. 2202, 6901.

Crepis nana Richards. 2206, 6905.

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Observations of Reptiles and Amphibians in a Louisiana Swamp

DONALD W. TINKLE
Texas Tech College, Lubbock, Texas

Few studies have been made of the reptiles and amphibians of a swamp. Two of these are the studies of Wright (1932) in the Okefinokee swamp of Georgia and a population study of *Thamnophis sauritus proximus* by Tinkle (1957) in Louisiana. This report contains a summary of observations and experiments made with several species in a cypress-gum swamp near New Orleans in 1953 and 1954. The study was conducted on the Tulane University Sarpy Wildlife Refuge in St. Charles parish. The habitat has been described in detail by Tinkle (*op. cit.*), including a report regarding vegetational changes and fluctuations in water level. Most of these data were obtained on 31 visits to the study area between November, 1953, and December, 1954 and were sometimes incidental to the population study of the western ribbon snake referred to above.

The water in the swamp is shallow (1-3 feet) except in borrow-pits traversing the refuge. There are open areas in the swamp resulting from timbering or representing abandoned oil well drilling sites. In these open areas cattail (*Typha domingensis*) and cutgrass (*Zizaniopsis milliacea*) predominate with pickerel weed (*Pontederia cordata*) in the shallow areas and water hyacinth (*Eichornia crassipes*) in the ditches. The swamp proper contains cypress (*Taxodium distichum*) and gum (*Nyssa aquatica*) with some ash (*Fraxinus sp.*) in the drier areas. Thickets of palmetto (*Sabal minor*) occur throughout the swamp. The dominant plants on the many ridges traversing the swamp are willow (*Salix nigra*), maple (*Acer drummondii*) and groundsel tree (*Baccharis halimifolia*) with blackberry (*Rubus* sp.) in the more open and disturbed areas.

Many parts of the swamp were investigated, but most observations were made along a ridge, 25 feet in width and 600 yards in length. At the end of this ridge was an abandoned wellsite consisting of open water, cypress swamp, and marsh flats, several ridges and deep ditches. This site was divided into 90 quadrats with aluminum tape, each quadrat 15 feet square. This area will henceforth be referred to as the study area and the ridge leading to it as the main ridge.

On each visit to the refuge notes were kept on the numbers of each species seen. On certain days attempts were made to survey and compare several areas within the swamp, to investigate in greater detail specific microhabitats, and to look for hibernating and egg-laying sites. The marking work was restricted to the study area although marked animals were searched for outside the quadrated area. All

animals were marked by toe clipping except the snakes on which the subcaudals were clipped.

A few general observations are included below, but the bulk of the data is treated under the species accounts.

General Observations

Influence of habitat on density

The ridges serve as a dispersal route for terrestrial species deep into the swamp; in fact, the richness of the fauna seems dependent upon the ridges and adjacent shallow water. Only the western cottonmouth (*Ancistrodon piscivorus leucostoma*) is abundant in the swamp proper. The speckled kingsnake (*Lampropeltis getulus holbrooki*), the gray rat snake (*Elaphe obsoleta spiloides*) and the eastern yellow-bellied racer (*Coluber constrictor flaviventris*) were seen on the ridges only, or occasionally in the palmetto flatwoods when these were unusually dry. The ridges were utilized by almost all species for basking, egg deposition or hibernation. The number of individuals seen in different microhabitats of each species, for which accurate data were kept, has been tabulated (Table I). The table indicates that the microhabitats generally associated with the swamp are the least productive while the ridges and marsh areas that are marginal or secondary and certainly comprising a small area of the swamp support much larger populations.

Water level fluctuation

The water level in the swamp fluctuated greatly; periodically, large areas were left relatively dry. In the study area (Fig. 1), the "marsh flats," consisting primarily of cattail and cutgrass, were dry, muddy, or covered with water up to one foot in depth. On several trips made under differing temperature conditions there was a clear correlation

Table I.—The numbers of several species encountered along the main ridge or in the study area from November 1953 to December 1954

Species	Pure Cypress-gum	Ridge	Purely Aquatic	Marsh
Ancistrodon piscivorus	25	23	6	19
Anolis carolinensis	8	96	3	104
Coluber constrictor	0	16	0	0
Eumeces fasciatus	2	53	0	1
Hyla cinerea	0	36	0	132
Lampropeltis getulus	0	15	0	0
Microhyla carolinensis	0	78	0	2
Natrix cyclopion	0	0	12	6
Natrix sipedon	3	6	25	12
Rana clamitans	15	675	7	165
Thamnophis sauritus	2	180	8	31
Totals	55	1178	61	472

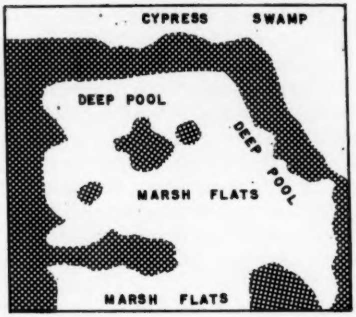

Fig. 1.—Study area in Sarpy Refuge showing the distribution of major microhabitats. Cross-hatched area is ridge or island. The ridge on the left is continuous with the main ridge discussed in text. (Scale: ¾ inch = 15 feet.)

between abundance of snakes in the study area and the amount of surface area covered by water (Table II). Seventy-three individual snakes seen in seven trips under wet conditions (10 per trip) compared with 19 encountered in 8 trips when the study area was relatively dry (2 per trip).

During these dry periods the amphibians and reptiles accumulate around remaining water holes where prey items such as frogs and small fish (mainly *Mollinesia*) become concentrated. On May 1, 1954, the study area was almost completely dry and no individuals were encountered. In another open ridge area of about the same size as the study area and located about one-half mile away in the same swamp, 25 snakes were found as well as a great number of amphibians. Rains during the following week raised the water level in the study area; nine snakes were encountered on May 8. Only 8 snakes were found in the area that had produced 25 the previous week.

Similar observations were made on several occasions in the swamp, but no data are available on how far reptiles may move to reach a more favorable environment as none of the marked animals were recovered far from the study area.

HIBERNATION

Hibernating sites in the swamp are mostly shallow and exposed. These include large, deep cracks that persist in the main ridge throughout the year; sites beneath the bark of logs and stumps, under boards and in rotting timbers or trees and in palmetto under the bases of the dead basal fronds that have pulled slightly away from the trunk of the plant; and in the bases of the cattail.

TABLE II.—The numbers of snakes encountered in the study area on trips during which the flats area was dry or covered with water

Temp. °F	55	60	65	70	75	75	75	77	82	82	85	85	85	90	90	Total:
Dry	0	1	0	0	0	3	0	1	3	0	4	0	0	7	0	19
Wet	4	0	4	0	9	0	0	0	0	8	0	15	24	0	9	73

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GENERAL OBSERVATIONS

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Anolis carolinensis	8	96	3	104
Coluber constrictor	0	16	0	0
Eumeces fasciatus	2	53	0	1
Hyla cinerea	0	36	0	132
Lampropeltis getulus	0	15	0	0
Microhyla carolinensis	0	78	0	2
Natrix cyclopion	0	0	12	6
Natrix sipedon	3	6	25	12
Rana clamitans	15	675	7	165
Thamnophis sauritus	2	180	8	31
Totals	55	1178	61	472

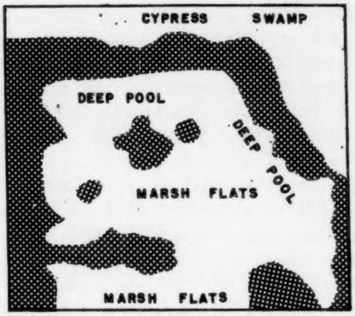

Fig. 1.—Study area in Sarpy Refuge showing the distribution of major microhabitats. Cross-hatched area is ridge or island. The ridge on the left is continuous with the main ridge discussed in text. (Scale: ¾ inch = 15 feet.)

between abundance of snakes in the study area and the amount of surface area covered by water (Table II). Seventy-three individual snakes seen in seven trips under wet conditions (10 per trip) compared with 19 encountered in 8 trips when the study area was relatively dry (2 per trip).

During these dry periods the amphibians and reptiles accumulate around remaining water holes where prey items such as frogs and small fish (mainly *Mollinesia*) become concentrated. On May 1, 1954, the study area was almost completely dry and no individuals were encountered. In another open ridge area of about the same size as the study area and located about one-half mile away in the same swamp, 25 snakes were found as well as a great number of amphibians. Rains during the following week raised the water level in the study area; nine snakes were encountered on May 8. Only 8 snakes were found in the area that had produced 25 the previous week.

Similar observations were made on several occasions in the swamp, but no data are available on how far reptiles may move to reach a more favorable environment as none of the marked animals were recovered far from the study area.

HIBERNATION

Hibernating sites in the swamp are mostly shallow and exposed. These include large, deep cracks that persist in the main ridge throughout the year; sites beneath the bark of logs and stumps, under boards and in rotting timbers or trees and in palmetto under the bases of the dead basal fronds that have pulled slightly away from the trunk of the plant; and in the bases of the cattail.

TABLE II.—The numbers of snakes encountered in the study area on trips during which the flats area was dry or covered with water

Temp. °F	55	60	65	70	75	75	75	77	82	82	85	85	85	90	90	Total:
Dry	0	1	0	0	0	3	0	1	3	0	4	0	0	7	0	19
Wet	4	0	4	0	9	0	0	0	0	8	0	15	24	0	9	73

Hibernation is mostly individual and most of the sites seem marginal, but are probably all that is normally required for the mild winters of southern Louisiana. However, mortality may be great during the rare exceptionally cold periods. The only aggregative hibernation occurs in the bases of the palmettos where insects are abundant and basking sites on the broad fronds are available. Here, large numbers of lizards and tree frogs may be found during the winter. Little mortality was observed in such sites; indeed, no predator can reach the animals while they are in the bases. Occasional individuals were found heavily infested with ants which are very common in most palmettos.

Egg-laying

The sites of egg deposition are discussed under the species accounts, but mention is made here of a device for obtaining eggs for study. Several V-shaped troughs were constructed and filled with humus, rotten wood, and earth and placed along the main ridge. Use was made of these for egg deposition by *Anolis* and *Lygosoma* to a significantly greater extent than surrounding areas (Gordon and Tinkle, 1959).

Species Accounts

Information was obtained on movement, growth, seasonal abundance, habitat preference, food, reproduction, hibernation, predation, mortality and behavior of many, but not all of the species, encountered.

Reptiles

Alligator mississippiensis

There were not sufficient deep water holes in the refuge to support many alligators. Two were seen on logs in a deep ditch paralleling the main ridge on March 13, 1954. Alligators were heard grunting on several occasions from a deep hyacinth-covered pond near the study area during showers in the spring and early summer. Some alligators were marked by tatooing the ventral scutes and released in this area in 1952; none was recovered and the above individuals may have been the ones seen.

Ancistrodon piscivorus leucostoma

Thirteen specimens were marked within the study area, but only one was recovered. This specimen, captured 5 times from November 15, 1953, to May 30, 1954, was perhaps the only one whose home range was primarily within the limits of the study area. This individual moved (straight-line) 120, 0, 90, and 75 feet between successive captures or an average of 71 feet. A polygon formed by connecting the outermost points of the capture of this snake encloses an area of 17,280 square feet or .40 acre.

The cottonmouth was seen on warm days throughout the year and was the first reptile in the study area to appear in the spring. Its peak density was reached between early March and late May. It

was less frequent in the area during the summer, but could be found in abundance at this season along the margins of the deep ditches. Many cottonmouths were found on the main ridge, but most of them were encountered in the swamp proper, particularly where deep water traversed the swamp in an area containing numerous fallen trees and stumps. These snakes were often out early in the year when the air temperature was 50-55° F. and no other species was out in the open.

Ovaries were removed from four females during the early summer. The body length (snout to vent) of these snakes was 410, 510, 615 and 635 millimeters. Only the latter two contained enlarged follicles and oviducts indicating sexual maturity. The largest contained 4 embryos, 3 in the right oviduct and one in the left. All of the ovulation scars were in the right indicating extrauterine migration of ova as reported by Tinkle (1957) in *Thamnophis sauritus* and by Legler (1958) in *Terrapene ornata.* The first young cottonmouths were found in the study area on October 10, 1954.

A hibernaculum of the cottonmouth was not found, but they were seen frequently during the winter around the crevices of the main ridge into which they often retreated when disturbed. These crevices probably serve as retreats during the infrequent cold weather in the area.

Anolis carolinensis carolinensis

Fifty Carolina anoles were marked and six recovered, five once and one twice. One female remained in the same quadrat from February 2-4, 1954. Four males, recaptured once, moved (straight-line) 50, 15, 15 and 45 feet over a period of 266, 7, 7 and 41 days, respectively. A male lizard recaptured twice moved 15 feet, staying within two adjacent quadrats over a period of 41 days.

No growth of significance was recorded. The greatest increment was 4 millimeters, but this is near the error in measurement. One case of natural digital loss was noted.

Anolis was seen on warm days throughout the year, but first became active in early February when the afternoon temperatures generally reach above 60°F. Mating was not observed until mid-April, but territorial behavior was observed early in February. Numerous instances of mutual attempts at bluffing were seen between male anoles, but none of those resulted in any altercation as the non-resident always moved out of the area when intimidated by the resident male. On one occasion an *Anolis* in a *Baccharis* bush began to bob and to display its dewlap when a *Eumeces* crossed the ground about three feet below the anole's position. The *Anolis* descended within 18 inches of the *Eumeces* and continued a vigorous bobbing. The *Eumeces* became stationary and remained so until the anole retreated to its original site. Later movement by the *Eumeces* elicited no further response from the male anole.

Anoles were most common on the more open areas of the ridges where they utilized the dense blackberry thickets and the buckbrush

as resting sites and in the flats where they stayed high on the stems of cattail and cutgrass. These lizards are quite common in areas that are frequently inundated and isolated from the ridges; the animals may reach these areas when the intervening spaces are dry, or nearly so. However, on two occasions anoles were observed to swim across 15 feet of open water when disturbed.

The unusual reproductive cycle of *Anolis* in this area has been discussed by Hamlett (1952). Some data on egg deposition were obtained in this study. Eggs were found throughout the summer under leaves, logs, and other debris on the ridges. A few were seen on the surface of the ground under blackberry clumps. Many eggs were collected, but only a few hatched. Three eggs measured on June 29, 1954, were 12.3 x 10.0, 12.8 x 10.0, and 11.8 x 10.0 mm. in greatest length and width. These hatched on June 30, July 9, and July 12 and the hatchlings were 22.0, 24.3, and 22.6 mm in snout-vent length. Four anoles, measuring 23.0, 23.6, 24.1, and 25.0, hatched July 19-24, 1954, from eggs that were 14.6, 13.1, 13.6, and 12.4 respectively. In all hatchings the eggs were slit along the side; in some the end was also opened. Other measurements of young anoles on the day of hatching were 24.7, 23.6, 25.0, 24.1, 25.0, 23.0, 25.2, 26.1, 25.0, 20.0, 25.0, 20.0, 23.0, 25.2, 26.1, and 24.7 mm. The average size at hatching for the 19 lizards above was 23.9 mm.

Anoles were found in a dormant, presumably hibernating state in fallen logs, rotting stumps, and in bases of palmettos. On February 20, 1954, 16 anoles were taken by two persons in one hour from palmetto bases adjacent to the study area. In addition 11 other lizards, 9 frogs and 5 mice (*Peromyscus*) were taken in the same shelters along with large numbers of ants, centipedes and millipedes. Further evidence of the importance of the palmetto to these lizards is attested by the fact that Mr. John Boley of New Orleans and I secured 525 *Anolis* and 100 *Lygosoma* together with uncounted numbers of *Hyla squirella* from the bases of these plants on two cold and rainy days in December, 1953, in an area similar to that of the study area, but with considerably more high ground.

No evidence of natural mortality of this species was noted, but numerous eggs of this species have been found in the stomachs of young *Lampropeltis getulus.*

Chelydra serpentina serpentina

Only one common snapping turtle was taken in the study area despite the fact that turtle traps were set in several locations. This animal was first caught on April 2, 1953, in shallow water and recaptured on February 4, 1954, 20 feet from the site of original capture. There had been no increase in size; on both occasions the turtle was heavily infested with leeches.

Coluber constrictor flaviventris

The eastern yellow-bellied racer was often encountered on the main

ridge, but never so deep in the swamp as the study area. It was always found in the more open areas of the ridge or along the open road embankments.

The racers first appear along the ridges in early February; they frequent the open areas for basking during the relatively cool spring. They often stay in the blackberry thickets or nearby *Baccharis* and retreat into the tangled vines when disturbed. After May the racers no longer frequent the open areas of the ridge where temperatures are high, but are found in the shadier sections of the ridges. A similar seasonal change was noted in the ribbon snake in this same area (Tinkle, 1957).

Racers were seen twice during the winter basking on the ground near the large crevices in the main ridge into which they took immediate refuge when approached.

Two egg clutches of this snake were found, both in seemingly marginal sites, on June 27, 1954, along one of the grassy road embankments. One clutch of six was found beneath a piece of newspaper and one of 15 was found under a small thin board: four eggs in the latter clutch had apparently been parasitized for the eggs were perforated by small holes.

Elaphe obsoleta spiloides

Four gray rat snakes were marked in the study area, but none was recovered. All of these snakes were found in trees or high bushes at least four feet off the ground; three were on the main ridge while the fourth was found in a rotten tree in the palmetto-cypress area about 10 feet off the ground. This last snake was found during a period when the ground was dry, but *Elaphe* could penetrate deep into the swamp in certain areas without touching the ground because of their remarkable climbing ability and the density of the vegetation.

One adult specimen was found dead and greatly emaciated in the study area on October 30, 1954.

Eumeces fasciatus

Seventeen five-lined skinks were marked in the study area, all within 6 quadrats. However, of the total captures of skinks (45), 38 were made within a single quadrat. This quadrat was characterized by containing many large flat boards, by little shading from 2 willows and 1 groundsel tree, and by an understory of sedges (*Carex*). One portion of this quadrat was about two feet higher than most other quadrats in the study area. Five of the seventeen skinks were not recovered, four were recaptured once, three twice, three on three occasions, one four times and one five times. Only three of the lizards were found outside the quadrat in which they were marked. One moved 60 feet (straight-line) along a contiguous ridge; another moved 15 feet to an adjoining quadrat. Twenty-six recoveries were made in the same 225 square feet in which the animal was marked,

indicating a relatively small home range. Fitch (1954) stated that the home range of this species in Kansas was approximately 90 feet in diameter for adult males and juveniles and 30 feet for adult females. In my area, movement and size of home range were restricted by water. The three lizards that had moved away from the quadrat in which they were originally marked averaged 40 feet in straight line movement, well below many of the movements recorded by Fitch (op. cit.).

The recaptures of skinks were made throughout the year, but in only two instances was it clear that the individual remained in the same quadrat several seasons. One of these, first marked in July 1954, was recovered for the third time in February, 1955, while the second was first captured in March, 1953, and for the fifth time in February, 1954. The other lizards, even though recovered in the same quadrat several times, were not seen again after a period of three months and had presumably moved to another area. Such movement from one area to another area was clearly shown to occur in this species by Fitch (1954).

A strong homing instinct was demonstrated by a *Eumeces* first caught on a small island in an otherwise permanently aquatic microhabitat and moved to a similar type microhabitat, 75 feet to the northwest, on February 4, 1954. On March 13, the lizard was found on the island where it was initially encountered, and again on March 14. It was necessary for this lizard to cross about 40 feet of open water to return to the island.

Outside the study area, *Eumeces* is found most abundantly in the [illegible] of the palmetto during the fall and winter. As many as 11 of these lizards were taken from palmettos in a one hour period. Of [illegible] *Eumeces* encountered in the study, [illegible] were on the ridges in or under [illegible] or rotting timber, one in the marshy flats, and [illegible] in rotten logs [illegible] in the swamp.

[illegible]

of the nest, eggs, or lizard at intervals. The female often emerged and basked under a light (placed above the terrarium), returning to the nest after varying periods of time. The nest temperature on 47 readings varied from 26.5°C. to 30.0°C., (avg. 28.4).

The light was turned on and off at intervals to determine the effect on the nest temperature. In several tests it was found that the nest temperature decreased one degree in an average of 152 minutes after turning off the light, but gained heat at the rate of one degree each 40 minutes after the light was turned on.

On three occasions it was possible to record the nest temperature immediately before and after the lizard had re-entered after basking. The temperature rose from 26.5 to 28.5° and from 26.7 to 27:5° within five minutes after re-entering; on the third occasion no change was noted in the temperature. On two of these occasions the temperature dropped slightly after re-entering and on the third, it continued to rise. These data indicate that the body heat of the lizard is held for a short time after re-entry into the nest.

Farancia abacura reinwardti

The western mud snake is probably one of the most abundant reptiles in the refuge, but is secretive and seldom encountered. Five of these were marked in the study area, but none was recovered. Three were caught in April, and one each in October and November.

The mud snake is a known predator of *Amphiuma*. One struggle between a six-foot snake and a two and one-half-foot salamander was observed in the study area. The snake had grasped the salamander in its mouth at about midbody and the two rolled over and over churning the water. The snake frequently attempted to swim toward the bank and to pin the salamander in order to work its jaws toward the head of the latter. The *Amphiuma* bit the snake in three places leaving deep, open cuts. Most mud snakes captured have numerous scars, presumably from similar encounters.

A *Farancia* found on the main ridge outside the study area laid 27 eggs on August 5, 1954. The eggs averaged 31.8 mm (28.0 — 35.0) in length and 21.1 mm (16.6 — 23.7) in diameter. This number of eggs is within the range of 20-30 that Meade (1946) reported as general in southern Louisiana.

A hatched clutch of nine eggs was found in the study area on October 3, 1954, under a rotten board. The eggs appeared to have recently hatched and two juveniles were found under adjacent boards. One of these was a male, 213 mm snout to vent, and the other, a female, 248 mm long. In both, the yolk sac scars were clearly evident. The eggs were in a shallow depression and had obviously been attended by the female for a considerable period because the depressions outlining her coiled body were clearly evident. The eggs were adherent to each other. This is in contrast with reports by Meade (1946) of eggs laid in captivity that were non-adherent. The adherence of these hatched eggs to each other could have been due to the drying of

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Outside the study area, *Eumeces* is found most abundantly in the bases of the palmetto during the fall and winter. As many as 11 of these lizards were taken from palmettos in a one hour period. Of 56 *Eumeces* encountered in this study, 53 were on the ridges in or under boards or rotting timber, one in the marshy flats, and 2 in rotten logs deep in the swamp.

Only one specimen of five-lined skink was found dead, this one beneath a board after a freeze in early February. No clear instance of predation on these lizards was found, but several young speckled kingsnakes disgorged eggs, some of which were thought to be those of this species.

The head of the male *Eumeces* becomes orange-red to salmon red in late March and early April. It reaches a maximum brilliance by the first part of June. The males never showed any territorial behavior. A single clutch of *Eumeces* eggs was discovered beneath a board on a high part of the main ridge. Mating was observed only once, on May 8, 1954. The details of the courtship were similar to those recorded by Fitch (1954) but copulation did not occur as the female successfully disengaged herself from the male.

A thermocouple was placed in contact with a clutch of seven eggs brooded by a female *Eumeces fasciatus* within rotting wood in a terrarium. From June 17, 1954 (date of capture of female and her eggs), until July 5 when the eggs hatched, temperatures were taken

of the nest, eggs, or lizard at intervals. The female often emerged and basked under a light (placed above the terrarium), returning to the nest after varying periods of time. The nest temperature on 47 readings varied from 26.5°C. to 30.0°C., (avg. 28.4).

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albumen, frequently spilled from eggs during hatching, but John Boley of New Orleans reported to me that he found a female mud-snake coiled about unhatched adherent eggs in south Louisiana.

Two *Farancia* were found dead in the study area. One of these, a juvenile, encountered on November 15, 1953, appeared to have been partly digested and then regurgitated by a predator. An adult found on April 2, 1953, was emaciated and apparently died of malnutrition.

Lampropeltis getulus holbrooki

Eighteen speckled kingsnakes were found in the refuge, all on ridges or along the road embankment. Seven of these were marked in the study area and two were recovered. One of these was marked at 1230 hours on February 4, 1954, and recovered at 1330 of the same day. During this time it had moved at least 90 feet, 75 of which was across open shallow water. The other snake was marked October 20, 1954, and recovered in the same quadrat on December 5, 1954. No growth occurred in the latter individual.

Kingsnakes were seen more commonly in the spring and summer. Only two individuals were found in the winter; both of these were basking near cracks in the main ridge into which they retreated when disturbed. These snakes were first seen in the area on February 4 and 13, 1954.

One kingsnake found beneath a log on November 20, 1954, had a cloacal temperature of 17°C. after 50 seconds; the temperature of the substrate beneath the log was 14°C. and the air temperature, 18°C.

Juvenile kingsnakes in the study area disgorged eggs of *Anolis*, of *Lygosoma* and possibly of *Eumeces*. One adult disgorged 11 eggs of *Pseudemys scripta elegans*, the most abundant turtle in the refuge.

Kinosternon subrubrum hippocrepis

Four *Kinosternon* were marked in the study area, but none was recovered. Two of these turtles, found on July 5, 1954, were attempting to dig, presumably for egg deposition. One of these had dug a shallow hole in the highest point of a quadrat on the main ridge and the other was digging into a rotten cypress log partially buried on one of the ridges. On two occasions mud turtles were active on the main ridge in February. The possibility that these two turtles were seeking egg laying sites is strengthened by the finding of a *Kinosternon* egg on the surface of the main ridge on February 20.

Four eggs of *Kinosternon* were found beneath a pile of boards on the edge of a low ridge on July 18, 1954, and six beneath a similar board pile in a low, sometimes flooded area. The latter group of eggs were laid as two singles and two pairs. The average size of these eggs was 29.6 mm in length (28.9 — 30.2) and 16.6 mm in diameter (16.4 — 16.7). A single egg was found beneath a board on June 6, 1954. The finding of eggs from February to July indicates an extended period of egg-laying.

Natrix cyclopion cyclopion

One male and one female were marked in the study area and 16 others were taken in other parts of Sarpy Refuge. The female was first captured April 10, 1954, and was recaptured, June 6, 1954, 80 linear feet from the point of original capture. This snake was noted as "possibly gravid" in the notes of April 10 and as "certainly gravid" when recaptured. During the period between captures the snout to vent length of the snake increased from 750 to 763 mm. The clipped subcaudals had almost completely regenerated.

Green water snakes are more common in the refuge than is indicated by their density in the study area. However, they are most frequently found in the deep water. The only item of food obtained from the stomach of these snakes was fish. The first green water snake seen in the area after the winter was observed on February 4, 1954, after several days during which the temperature had reached 70°F.

One female caught on May 8, 1954, measured 790 mm snout to vent and contained 18 embryos. Young green water snakes were never seen in the refuge.

A possible polyandrous mating aggregation of these snakes observed near Lafayette in southern Louisiana has been reported in detail elsewhere (Tinkle and Liner, 1955).

Natrix rigida

One *Natrix rigida* caught beneath a board in the study area was never recovered, nor was another that was caught in a ditch beside one of the shell roads in the area. This latter snake disgorged a crayfish when captured.

Natrix sipedon confluens

Six broad-banded water snakes were marked in the study area. Three were caught in the deep water ditches, one basking on a log over deep water, and two under boards on a ridge bordering a deep pool. One of these was recovered on November 3, 1954, in the same quadrat in which it was marked October 30. It seemed torpid (air temperature, 17°C.) when taken on October 30, but it may have been in poor physical condition because it was dead when found on November 3.

Forty-six broad-banded water snakes were captured in the refuge. Three of these were found in the cypress swamp, 6 on ridges, 12 in marsh flats, and 25 in deep water situations. This snake first appeared active in late February and the last exposed individual was encountered in early December.

An aggregation of *Natrix sipedon confluens* was observed in the study area on April 10-11, 1954. Ten snakes swam nervously about, each continuously nosing any other snake swimming close to it and showing uncommon interest in movements of the water made by the observer. This was interpreted as a search for mates on the part of

male snakes, although only one female was found near the pond. On the same dates this curious phenomenon was observed by Mr. Ernest Liner in Lafayette Parish, La. These two occurences have been discussed in detail (Tinkle and Liner, 1955). This same pattern was observed in the study area and in the same pools by Mr. Whitfield Gibbons in 1955 (no specific date except "spring") and by Mr. John Boley on April 28, 1956. Mr. Boley reported seeing 12 *confluens* in one pond on the study area and 8 others engaged in similar behavior in a deep pool bordering the main ridge. All snakes involved were described as "small" and slender, and were probably males. The annual repetition of this pattern of behavior indicates that this is a regular part of the mating preparation in this water snake.

The smallest sexually mature female examined measured 580 mm snout to vent. Eleven mature females from the refuge were examined and the number of potentially ovulatory follicles in the ovary or the number of oviducal embryos was counted. There is an apparent direct correlation of size of the female to the size of the brood (Table III).

In a female taken on April 10, 1954, there were 11 preovulatory follicles greater than 12 millimeters in greatest length; a female taken on April 24 contained 27 such follicles greater than 16 mm in length. The first gravid females were taken May 1. Three gravid females collected on June 27 had embryos with scales and color pattern developed.

Only two males were examined for the presence of mature spermatozoa. One of these (snout vent length of 520 mm) captured June 6, 1954, contained masses of active spermatozoa in the testes. A second specimen captured June 27 (length of 415 mm) was sexually immature and contained no spermatozoa.

Opheodrys aestivus

The Sarpy Refuge appears to be an excellent habitat for *Opheodrys* because of the profusion of blackberry on the ridges, a habitat in which large series of these snakes have been collected in other areas of southern Louisiana. However, only three specimens were found on the refuge and only one of these was marked in the study area. The latter was never recovered. This marked individual was found on

TABLE III.—The relationship between body length in millimeters and the size of the brood in *Natrix sipedon confluens*

Body length (snout to vent)	580	605	622	625	670	675	675	680	700	704	790
No. follicles or embryos	11	10	16	15	13	13	17	20	22	16	27
Average (Bl — Brood)			630 — 13						710 — 20		

October 30, 1954, on the upper fronds of a cattail in shallow water. The cloacal temperature of this snake was 20°C. at an air temperature of 17°C. The other two captures were made in blackberry thickets in other areas of the refuge on June 6 and on June 27, 1954. On both days the temperature was 27-28°C.

Pseudemys scripta elegans

This turtle was never seen in the study area, presumably because of the absence of any extensive deep water. In many areas of the refuge, in the borrow ditches along the shell roads and in deep swamp ponds, they were abundant. None of these turtles was marked, but some interesting observations were made on nesting and nest predation.

Between June 27 and July 18, 1954, 35 *Pseudemys* nests were discovered in the refuge. These were all along the road embankments near the borrow pits; of these only one nest had not been opened by a predator and this one contained eight eggs.

It is not known what animals ate the eggs, but raccoons and minks are the most abundant carnivores in the swamp. How these animals manage to find the turtle nests is not clear, but Cagle (1950) reported that egg hunters in southern Louisiana believe that the cloacal contents which the female turtles empty into the nest attract the predators. Cagle (*op. cit.*) has also recorded an extreme instance of predation on a swamp ridge in southern Louisiana on which more than 500 disturbed and only one undisturbed nests were found.

Thamnophis sauritus proximus

Two hundred and twenty-one western ribbon snakes were encountered in the refuge from November, 1953 to December, 1954, and many others were examined from similar habitats elsewhere. The data relative to the ecology, growth and reproduction of these animals has been presented elsewhere (Tinkle, 1957) and no other data are available.

AMPHIBIANS

Amphiuma means

The taxonomic treatment of this salamander employing the largest series has been that of Hill (1954) and I follow her in treating *Amphiuma means* as non-conspecific with *A. tridactylum*. Two *Amphiuma means* were seen in the study area. One large individual was seen in a struggle with a *Farancia* as reported above and a second was seen several times under a board in a partially submerged quadrat.

Observations were made periodically by Mr. John Boley of New Orleans and by me of two *Amphiuma* populations in Audubon Park, New Orleans, New Orleans Parish, and in the western part of that city of Jefferson Parish. The salamanders in the Audubon population remain in their burrows beneath the shallow water of a drainage ditch

and extend their heads a short distance into the water. They are extremely sensitive to vibrations of the ground above them and will withdraw their heads immediately when approached. The lights that are used to find the *Amphiuma* apparently disturb them very little. In the park ditch there is little vegetation and the salamanders are rarely seen completely out of their burrows, except when the entire park is inundated by torrential rains.

The Jefferson Parish population occupies a similar ditch beside a railroad track; the ditch contains cattail and in places in overgrown by alligator weed, *Alternanthera phylloxeroides*. The salamanders are usually out of their burrows and show no tendency to move when approached. Even those that are in burrows are not disturbed by vibrations of the earth above them. Apparently proximity to the railroad tracks has conditioned them to vibrations and the heavy growth of weeds may account for their being out of their burrows most of the time, since the weeds partially substitute for the cover provided by a burrow.

Bufo valliceps valliceps

Only four Gulf coast toads were found in the refuge, but this toad is quite abundant in some nearby areas where it breeds in temporary rain pools. At least one of the four toads examined showed a strong morphological similarity to *Bufo fowleri*. Other observations of large samples of toads from New Orleans in 1953 and 1954 clearly showed evidence of morphological overlap and presumable hybridization.

None of these toads was taken in the study area; all were found under boards in open areas of the main ridge or the larger open areas around well sites.

Hyla cinerea cinerea

Fifty-three green tree frogs, one of the most abundant animals in the swamp, were marked in the study area, but only five were recovered. Each was recaptured a single time. The shortest time that elapsed between recoveries was 7 days, the longest, 33. Three recoveries were made in the same quadrat in which they had been marked and two were found in an adjacent quadrat, a maximum straight line movement of 15 feet. The greatest size increment in the recovered frogs was 2 mm, probably within the degree of error in measurement.

Of 168 *Hyla cinerea* encountered in the refuge exposed, 36 were on ridges, usually on *Baccharis* branches and 132 in the marsh flats where they occurred almost exclusively on *Typha*. Only a few were found on *Zizaniopsis* which may be avoided because of its cutting edge. Thirty of these frogs were found on the fronds of palmetto, often in between two fronds that were close together or in the recesses of a folded frond. With few exceptions the treefrogs encountered on the ridges were there during the colder parts of the year. These frogs were often found in a torpid state in rotten logs and stumps.

Hyla cinerea also hibernates in the bases of palmettos; they were

often found in the winter by stripping away the dead portion of the outermost basal fronds. On February 20, 1954, eight of these frogs were found in this way. Usually, *Hyla squirella* is much more abundant in these situations than *H. cinerea,* but the former species was encountered only once in Sarpy Refuge.

Occasional *Hyla cinerea* are found between the leaves at the base of cattails. On warm days these individuals emerge to bask, but those in logs and stumps never seem to emerge during the winter. The frogs in the cattails are possibly more subject to mortality from rapid weather changes, but none was found dead in these sites.

One *Hyla cinerea* was found dead in the crotch of a *Baccharis* bush on November 29, 1953, and another was found on the top of a large palmetto frond on October 21, 1954, with one leg missing and a hole in one side of the body. It appeared to be the victim of a predatory bird.

Microhyla carolinensis carolinensis

Thirty-three eastern narrow-mouthed toads were marked in the study area. All of these were taken on high ridges in five quadrats and 23 of them were taken in a single quadrat containing a lot of boards. These boards were numbered so that movement of the animals within a small area could be detected. Two of the marked animals had naturally mutilated toes and these were incorporated into their numbers.

Seven microhylids were recovered; five of these were recaptured once after a lapse of 9, 7, 5, 7, and 18 days. The records span every season of the year. All were recovered in the same quadrat in which they were marked and none showed a size increase greater than 2 millimeters which is within the range of error of measurement. Within this quadrat the toads had moved from one board to another. Two of the toads were recovered three times in the same quadrat, but under different boards each time. One of these was first marked on February 2, 1954, and the other on March 16, 1954. The other was first found on March 14, 1954, and recovered for the third time on July 18, 1954. Neither individual grew during this period. None of the above movements exceeded 10 feet (straight-line.)

Two instances of regeneration of clipped toes were noted. One toad showed regeneration of one-half of the clipped digits after 113 days and another partial regeneration after 55.

Eighty of these toads were found in the refuge, of which 78 were on ridges under cover of boards or logs and two in the marsh flats. From November to January an average of 1.7 toads per trip were captured, from February to April, 2.0, from May to July, 1.7 and from August to October, 2.0. There appeared to be little seasonal variation in abundance. The only mating aggregation was observed May 8, 1954, when six pairs were found in amplexus.

Anderson (1954) showed that the peak size groups in most microhylid populations studied by him was between 23 and 28 millimeters

in snout to vent length. He examined some samples from the Sarpy Refuge that he thought showed a different size group composition than those from populations in open areas. My data on 32 specimens partially substantiate this idea as the high peak in this sample of 32 was near 21 mm, with smaller peaks between 22 and 28 mm. The mean size of this sample was 23.0 mm, an average near Anderson's figures for individuals in the second year class.

Rana catesbeiana

The bullfrog is not abundant in the swamp; only 30 individuals were encountered in the refuge. None of these amphibians was marked.

The first individual encountered in the study area was found March 13, 1954. It was the victim of bird predation. The head was badly mutilated by what appeared to be bill marks. A second individual, encountered on June 6, 1954, had been opened ventrally and almost eviscerated. The only concentration of bullfrogs in the study area was observed in late June during an extreme dry spell when a dozen individuals congregated around a pond covering four quadrats.

One adult bullfrog was found under a board in a quadrat on October 21, 1954. The frog was in a depression beneath the board and remained there until early January when the observations were terminated. This was apparently its hibernation site.

The bullfrog was heard calling on only one occasion during a hot dry period on June 6, 1954.

Rana clamitans

On several occasions a census was taken on *Rana clamitans* by direct count in the study area. One count revealed 15 in the cypress swamp, 7 in purely aquatic sites, 165 in the marsh flats and 675 in the ridges near water. These frogs were not marked despite their abundance because marking work with them would have precluded attention to any other species.

Through two winters in the study area, only juveniles were seen. The last adults were observed exposed in October, 1953, and November, 1954, and they reappeared in February of both years. From February through April the adults are abundant, although they are apparently distributed differently from the juveniles because they are seen most often along the margins of deep water, while juveniles are most abundant in more exposed locations along the edges of shallow water or out in the march flats. By May 1 the adults become sparse and are not seen again in numbers until the following year.

A breeding group of *Rana clamitans* was not observed in the refuge, but tremendous tadpole concentrations of this species were found on numerous occasions in April and May. The adults breed in the landlocked temporary rain pools in the cypress swamp and in the permanent pools of the area. The temporary pools are subject to

rapid drying and enormous masses of dead or moribund tadpoles of this species have been found.

Rana clamitans is primarily prey for the ribbon snake and cottonmouth in this area.

Other Species in the Refuge

Because of the paucity of published herpetological records from south Louisiana, the following species encountered in the refuge for which no important data are available are included as locality records.

REPTILES	AMPHIBIANS
Terrapene carolina triunguis	*Acris gryllus gryllus*
Lygosoma laterale	*Hyla squirella*
Lampropeltis doliata amaura	*Hyla versicolor versicolor*
	Rana grylio
	Rana pipiens

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The Forest-Prairie Ecotone in Northeastern Illinois[1]

PAUL D. KILBURN
San Fernando Valley State College, Northridge, California

This paper describes the vegetation of pre-settlement times in Kane County, Illinois, and discusses its composition and pattern of distribution as shown by the General Land Office Survey notes. The "pre-settlement vegetation," or the plant cover which prevailed prior to human modification by settlement, is a strong influence on the land settlement and land use pattern of an area.

Kane County is situated in northeastern Illinois about 30 miles west of Lake Michigan and 25 miles south of the Wisconsin border. The county contains 513 square miles and the topography is modified by the irregular deposition of glacial material. A prominent morainal system bounds the Fox River, the main drainage system of the county, creating a narrow, but prominent, valley (Fig. 1). The remainder is, for the most part, gently rolling and well-adapted to farming, although the northern half of the county is hillier and more dissected by ravines than the southern part. Rainfall in the region averages 34 inches a year and the mean annual temperature is about 48°F. (U.S.D.A., 1941).

The county is located at the edge of Transeau's (1935) 'Prairie Peninsula' in the transition region between the prairie and forest, and it is because of this ecotonal position that the area was chosen for study.

Methods

The presentation is based upon data from the General Land Office Survey, performed here between 1837 and 1841. Use of the General Land Office Survey notes to reconstruct pre-settlement vegetation has been amply discussed by Bourdo (1956) who details at some length both the advantages and disadvantages of this technique. Bourdo concludes that an accurate and precise picture of the original vegetation can be depicted through careful use of these notes.

In essence the data transcribed by the surveyor in these surveys is a tree sampling along the mile-square section lines. The distance and direction to the nearest sizeable tree in each quadrant was recorded at the corners of the mile-square sections. Other trees along the section line were noted less regularly, while the location of the transition between vegetation types was precisely recorded as to distance from the previous section corner. A summary of this information allows the investigator to construct a map of the existing vegetation types as well as detail the relative abundance and size of tree species.

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[1] This paper is a revision of the author's unpublished Master's Thesis (Kilburn, 1954). The reader is referred to this study for a fuller discussion of the subject.

TABLE I.—Summary of individual bearing tree data as recorded in the General Land Office Survey, Kane County, Illinois

Classes *	4 & 5	6 & 7	8 & 9	10 & 11	12 & 13	14 & 15	16 & 17	18 & 19	20	22	24	26	28	30	36	40	48	Total	Percent of Total	Basal Area	Percent Basal Area
Bur Oak	3	28	82	180	301	101	70	219	153	6	120	1	6	63	4	4	1	1342	63.81	2102.58	61.91
White Oak	—	5	12	37	70	26	21	71	91	5	60	—	1	38	6	3	—	446	21.21	922.51	27.16
Red Oak	1	2	10	10	17	4	3	14	7	1	5	—	—	—	—	—	—	74	3.52	89.60	2.64
Sugar Maple	—	1	5	7	24	3	2	3	5	—	7	—	—	2	—	—	—	59	2.82	78.62	2.32
Hickory	—	2	2	11	17	1	1	3	2	—	2	—	—	—	—	—	—	41	1.95	38.25	1.14
Ash	—	1	2	8	17	2	—	4	—	—	4	—	—	1	—	—	—	39	1.85	45.29	1.33
Elm	—	—	1	4	4	3	3	2	—	—	4	—	—	2	—	—	—	23	1.09	38.99	1.15
Ironwood	—	2	1	17	3	—	—	—	—	—	—	—	—	—	—	—	—	23	1.09	12.37	.36
Basswood	—	—	1	2	10	1	2	5	—	—	—	—	—	—	—	—	—	21	1.00	21.99	.65
Walnut	—	1	—	—	3	2	—	2	2	—	2	—	—	—	—	—	—	12	.57	22.97	.68
Cherry	—	—	1	—	3	—	1	—	—	—	—	—	—	—	—	—	—	5	.24	4.10	.12
Pin Oak	—	—	—	—	1	—	—	2	2	—	—	—	—	—	—	—	—	5	.24	8.68	.25
Hawthorn	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	3	.14	1.88	.06
Poplar	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	3	.14	1.92	.06
Maple	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2	.09	1.09	.03
Hackberry	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	.09	.89	.03
Cottonwood	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	.05	1.40	.04
Sycamore	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	.05	1.77	.05
Willow	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	.05	.54	.02
TOTAL																		2103	100.00	3396.04	100.00

* Two-inch diameter classes.

The General Land Office Survey of Kane County was performed under the special instructions of 1834 which applied to both Illinois and Missouri (Stewart, 1935). At this time, according to the survey, only a few settlers had established farms or saw-mills and the vegetation present was unmodified by settlement. The influence of the Indian on the vegetation is not known, although Day (1953) has shown it to have been considerable in New England.

In this survey, four "bearing" trees were cited at each section corner, two at the midpoint of each section line, and two or three "line" trees at irregular intervals along the section line. Around each section, as a result, the name, size and distance away from prescribed points were noted for more than 30 trees, when the section was forested. In the entire county 2103 trees were recorded (Table I).

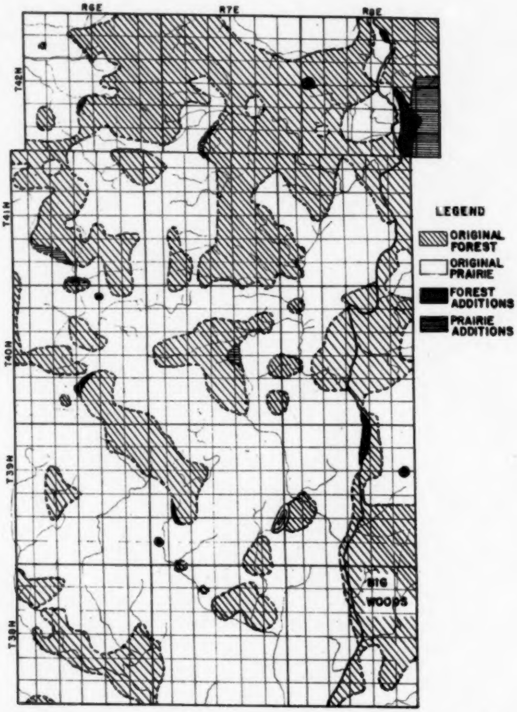

Fig. 1.—Pre-settlement forest and prairie cover in Kane County, Illinois as mapped by the General Land Office Survey (1837-1841) and modified by the author. The forest is indicated by black and single cross-hatching, the prairie in white and horizontal cross-hatching.

In prairie areas, where no trees were growing, the corners were marked with posts set in mounds. Beneath the posts, charcoal was placed to preserve location of the spot.

Inasmuch as the common names of the trees were used by the surveyors, it is important to assign scientific names with some care. The author's interpretations are given in Table II. Little difficulty was encountered in these interpretations inasmuch as the most abundant species are common today in local woodlots. Furthermore, similar translations in Wisconsin (Cottam, 1949; Stearns, 1949) and Indiana (Finley and Potzger, 1952) support the interpretations made here. For more complete discussion of individual determinations see Kilburn (1955).

RESULTS

The information gleaned from the surveyor's notes has been mapped and compared with the morainal systems of the county, the soil types and the topography. Figure 1, the map of the major vegetation types, summarizes the information obtained from the Survey notes. Construction of the map was not difficult for the notes indicated the type of vegetation at each section and quarter corner. If forested, bearing trees were recorded; if the corner was in the prairie, it was so noted. In addition, as the surveyors traversed a section line, they recorded the exact distance from the preceding corner that they passed out of the forest into the prairie, or from prairie to forest. Thus,

TABLE II.—Species identification from General Land Office Survey data

Surveyor's Entry	Common Name	Probable Species (Fernald, 1950)
B. Oak	bur oak	*Quercus macrocarpa* Michx.
W. Oak	white oak	*Q. alba* L.
R. Oak	red oak	*Q. rubra* L.
P. Oak	northern pin	*Q. ellipsoidalis* E. J. Hill
Sugar	sugar maple and black maple	*Acer saccharum* Marsh. and *A. nigrum* Michx.
Ash	ash	*Fraxinus* spp.
Elm	elm	*Ulmus* spp.
Ironwood	ironwood	*Ostrya virginiana* (Mill.) K. Koch
Lynn	basswood	*Tilia americana* L.
Walnut	black walnut or butternut	*Juglans nigra* L. or *J. cinerea* L.
Cherry	black cherry	*Prunus serotina* Ehrh.
Haw	hawthorn	*Crataegus mollis* Scheele
R. Haw	red haw	
Poplar	cottonwood	*Populus deltoides* Marsh.
Maple	silver maple	*Acer saccharinum* L.
Hackberry	hackberry	*Celtis occidentalis* L.
Cot	cottonwood	*Populus deltoides* Marsh.
Sycamore	sycamore	*Platanus occidentalis* L.
Will	black or peach-leaved willow	*Salix nigra* Marsh or *S. amygdaloides* Anderss.

by merely connecting these transition points, an accurate map of the two structural types of vegetation, forest and prairie, was constructed. Precision, however, diminished directly in proportion to the distance from the section line, since the interior of the section was not traversed, and forest boundaries were undoubtedly drawn in by inspection by the surveyors. For this reason, the degree of refinement in the interior of the sections of the map is limited to visual inspection by the surveyor, modified by the correlation with soils and other present-day information.

The map agrees closely with the one prepared by the surveyors summarizing their field notes. This latter map, accompanying their notes, omitted several small groves of trees cited in the notes, and misrepresented the prairie-forest border in T24N R8E. In general, however, it was reliable and fairly accurate.

The map denotes the pattern of prairie and forested land. Forest covered 38.3 percent of the land; the remainder was grassland or prairie. Forest existed in all townships, but the map clearly shows the transition from the extensive prairies in the southwest portion of the county to the extensive forests in the northeast. This gradation points directly to the prairie heartland of Western Illinois and illustrates that Kane County exemplifies the forest-prairie ecotone, with the areas adjacent to the main prairie areas predominantly grassland and the peripheral areas mostly forested.

Prairie has not been broken down into separate types inasmuch as the surveyor's notes examined in Geneva[2] mentioned nothing of either the composition or structure of this grassland. Conard (1952) has listed many prairie types and discussed use of the term 'prairie' in some detail. Sampson (1921) has shown that *Andropogon gerardi* dominated the mesophytic prairie areas in Illinois, while several prairie types still persist in Wisconsin (Thompson, 1940).

Three distinct forest types existed at the time of the survey. The three forest types found are a bur oak type, by far the most abundant; a flood plain type, confined primarily to the Fox River Valley and stream banks; and a more mesophytic white oak - sugar maple type located just east of Aurora. These types can be located in Figs. 2, 3, and 4 by inspection. Data for the types are given in Table III.

DISCUSSION

The bur oak type covered the largest portions of the forested areas in the county. Bur oak and white oak constitute the dominants of this type. Together these trees formed over 85 percent of all the bearing trees in the entire county, while in each of the three northernmost townships their occurrence exceeded 95 percent (Fig. 2). Stands of this type persist today and it can be seen that they were often savanna-like oak-openings similar to those described by Stout (1944) for south-

[2] These notes residing in the county seat, Geneva, are copies of the original set on file at the State Capitol of Springfield.

TABLE III.—Kane County forest composition by forest type

Tree *Species*	Flood Plain *Number*	*percent*	Mesophytic *Number*	*percent*	Xerophytic *Number*	*percent*	Total
Bur Oak	0	0	30	13.3	1312	73.3	1342
White Oak	0	0	79	35.1	367	20.5	446
Red Oak	8	9.1	18	8.0	48	2.7	74
Sugar Maple	5	5.7	50	22.2	4	0.2	59
Hickory	5	5.7	8	3.6	28	1.6	41
Ash	18	20.4	15	6.7	6	0.3	39
Elm	13	14.8	3	1.3	7	0.4	23
Ironwood	12	13.6	8	3.6	3	0.2	23
Basswood	12	13.6	3	1.3	6	0.3	21
Walnut	7	8.0	4	1.8	1	0.0	12
Other	8	9.1	7	3.1	8	0.5	23
Total	88	100.0	225	100.0	1790	100.0	2103

ern Wisconsin. Cottam (1949) describes these open glades as containing about fourteen large, open-grown trees to the acre and possessing a ground cover of prairie forbs and grasses. There was, however, an abrupt transition between forest and prairie. It was usually a matter of a few steps between the two and the surveyor had little difficulty in depicting the boundary.

The bur oak type is best considered a 'woodland' rather than a 'forest,' as the former term applies to open-grown stands of trees. The first term is more suitable than the word 'timber' used by the surveyor.

The bur oak is described by the Society of American Foresters (1954) as a "pioneer type on the edge of the prairies being gradually succeeded by northern pin oak (*Quercus ellipsoidalis*)." Such a situation did not occur in this county, and I believe that actual conditions here are more accurately depicted by Braun (1950), who includes this area in an oak-hickory forest region and classifies the type as one in which bur oak is dominant or co-dominant with white oak. This is precisely the condition found in Kane County, and here the bur oak or bur oak - white oak type is the forest of the prairie-forest ecotone. The particular role of white oak in this relationship has not been determined from this study. It apparently expresses a greater degree of mesophytism than bur oak, for it is much more prevalent than the latter in the "Big Woods" area, the name given to the wooded area east of the river in Tiers 38 and 39 North, R8E, and now largely occupied by the city of Aurora. Whether white oak is succeeding bur oak, or whether there is any successional relationship between the two, is not apparent.

The flood plain forests are heterogeneous in Kane County, and, owing to the paucity of sample data in such area, it is not possible to define sub-types here nor even detail the dominants. This forest formed a lowland border to the Fox River and stretched continuously through the county. It penetrated the interior of the county only along the larger streams.

Data for the Big Woods suggest a far more mesophytic forest than the bur oak type. In over-all numbers it is dominated by white oak, with sugar maple, bur oak, and red oak remaining important constitutents. Such a forest type generally resembles that described by Braun (1950) as the more mesophytic white oak-sugar maple admixture of this region. The Big Woods area, however, covers several thousand acres, and it would be illusory to classify this as a homogeneous forest type in view of the heterogeneous topography and drainage which often produces localization of individual species in this area. The survey data are not refined enough to actually pinpoint localized subtypes, however, and no such attempt will be made in this paper.

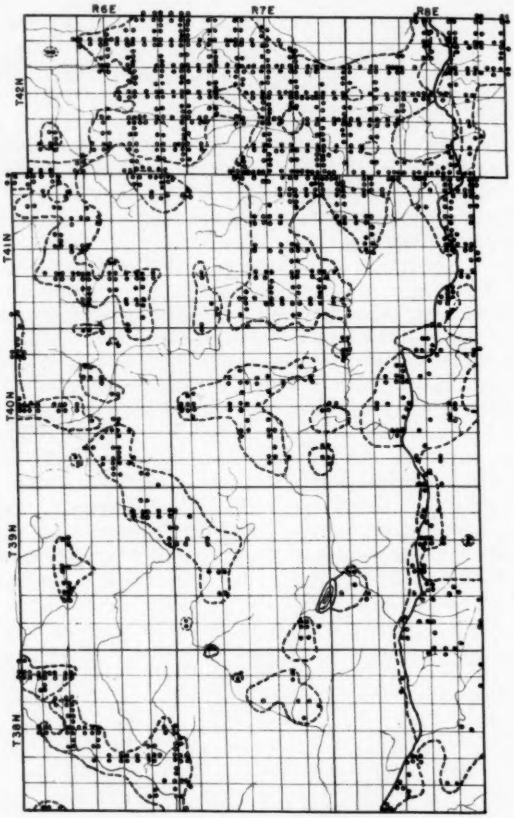

Fig. 2.—The distribution of bur oak in Kane County, Illinois as shown in the General Land Office Survey (1837-1841).

Four soil classes were originally described in the county (Hopkins *et al.,* 1917): (1) upland prairie soils, (2) upland timber soils, (3) terrace soils, and (4) swamp and bottomland soils. The first two types cover about three-quarters of the county and are often derived from identical parent materials, but present marked differences. The timber soils are true podzolic soils. They possess little organic matter, are light in color, highly leached, and originally supported forest vegetation. The prairie soils contain considerable organic matter, possess a topsoil which is nearly black, are only slightly leached, and originally supported prairie vegetation (Wilde *et al.,* 1949). The distribution of these soils is nearly identical with the corresponding vegetation boundaries. This coincidence is so remarkable that refinement and substantiation of several questionable areas of the vegetation were made (such as those of T42N R8E).

The line separating these two soil associations is not always clear cut, for gradations do occur (Wascher *et al.,* 1950). Certain soil types,

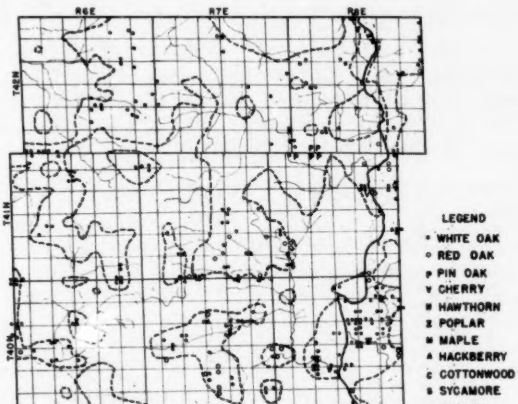

Fig. 3.—The distribution of white and red oak, and uncommon trees as shown in the General Land Office Survey (1837-1841).

as Virgil Silt Loam (104) represent transitions between prairie and forest soils. At the time of the survey, the vegetation of such areas is described as "recent forest encroachment on prairie" and indicates that the forest existence in these areas has not been maintained long enough to convert the soil to true podzolics.

Existence of such areas lends support to Gleason's (1922) suggestion of climatic shift and forest advancement in this region. No soil types for the county are mentioned which indicate prairie advance upon forest vegetation.

This comparison of vegetation and soil maps is by no means as satisfactory as detailed field analysis would be. It is hoped that such field work will be made in the future in order to better clarify the basic vegetation - soils relationship.

This topography of the land exerts marked influence upon temperature, humidity, wind and drainage, thereby strongly affecting soils and soil moisture. Such features often radically influence the vegetation. By plotting the vegetation types upon detailed topographic maps of the various quadrangles, certain distributional features become evident.

1. The northern half of the county is more highly dissected by hills and ravines than the southern half. This pattern corresponds to the vegetation distribution pattern, the northern area being more heavily forested than the gently rolling southern portion.

2. The prairie patches in T42N, Ranges 7 and 8 East, prevail over flat areas.

3. Forest patches generally cling to stream beds. Ravines and valleys encourage forest formation by providing protection from searing winds and frequent prairie fires. In addition, moisture conditions are often better, both as a result of this protection and also as abetted by infiltration of ground water from adjacent uplands through intersection of the drainage table. The persistence of forest in ravines in Iowa is well depicted by Shimek (1948).

4. The river bluffs, where gradients are steep, are almost invariably forested. Where these gradients lessen the prairie often extends to the river border.

5. The east side of the river — in the lee of the prevailing winds — is more heavily forested than the west side, although topographic differences are slight.

These generalizations are by no means universal within the county. The prairie often extends over steep hills while the forest sometimes occurs on level terrain, but as a rule the above holds true.

Perfect correlation between topographic and vegetational boundaries is not expected, for an area of rough terrain could well act as a reserve center from which the oaks could advance outward into the

prairie in times of favorable tree establishment. This phenomenon is suggested by the forests found on level land west of a major moraine in T 41 and 42N, R7E. But it is apparent that in Kane County the topography strongly affects the distribution of the vegetation.

The extent of the effect of prairie fires on the existence and maintenance of the prairie has been debated for some time. Presumably started by Indians or lightning, such fires, fanned by the hot and steady westerlies, swept rapidly eastward in the dry seasons. These fires certainly had some effect on the vegetation (Curtis and Partch, 1948), but the extent of such influence is not clear (Shimek, 1948 and Transeau, 1935). Extensive prairie fires would tend to promote prairie vegetation on the western borders of such obstacles as streams, lakes, and rivers. Such a condition is found to be generally true in the southern part of the county where the forest is more abundant on the eastern banks of the streams. The same holds true with regard to the Fox

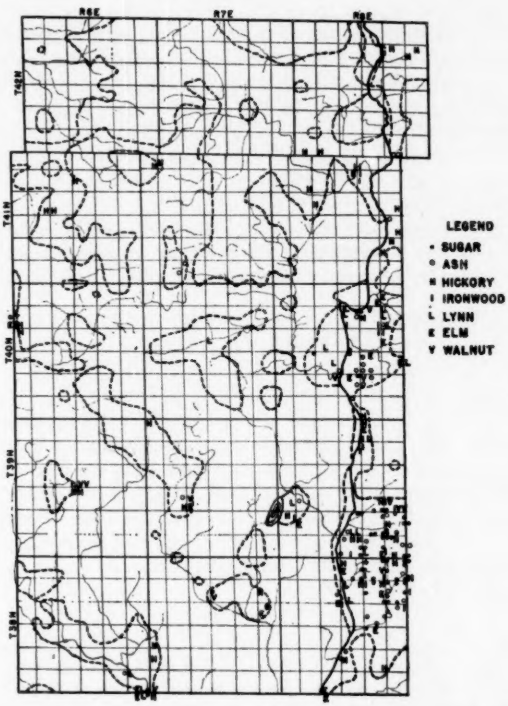

Fig. 4.—The distribution of sugar maple and other mesophytic trees in Kane County, Illinois as shown in the General Land Office Survey (1837-1841).

River. Evidence in this county is favorable to the theory that fire exhibited some influence upon prairie distribution.

The evidence is far from conclusive, however. First of all, the area is small and the pattern may be the result of chance. Secondly, the ravines of these streams and the river may have been acting as a windbreak and not just a firebreak. Such protection from the searing westerlies would favor forest establishment upon the leeward bank, for this side is less subject to desiccation and seedling mortality.

SUMMARY

The original land survey of the Middle West has provided us with a regular, independent sampling of extensive areas of forested vegetation prior to any major modification by the early settler. The data from these surveys provide a basis for mapping broad types of vegetation as prairie and forest, and permit the careful student to refine these types considerably.

The methodology of the early survey imparts limitations and difficulties of interpretation which must not be overlooked. For example, care must be taken in the identification of species from common names.

The original forest vegetation of Kane County consisted largely of oak openings, composed of pure bur oak or bur oak - white oak stands. Lowland and swamp forests did occur along the river and stream bottoms, while a more mesophytic forest was found on the heavier soils of the Big Woods area. Over three-fifths of the county was originally covered with prairie.

The boundaries between prairie soils and forest soils were nearly identical with the corresponding vegetation boundaries, indicating that soil formation in this region responds directly to vegetational differences.

Topographical differences account for the distribution of much of the vegetation. The more level areas, subject to both wind and fire, were normally prairie habitats. Protected ravines, valleys, steep bluffs and hills were largely forested. There are, however, many areas where the vegetation pattern cannot be explained by topographic variation.

The final conclusion reached in this study is that there is no simple explanation for the distribution and co-existence of forest and prairie in this ecotonal area. Although a single environmental feature may be primarily responsible for a vegetation type predominating in a specific area, the precise distributional pattern over the entire county can be explained only as the result of the interplay of several factors.

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The Distribution of Some Snakes in Mississippi

J. WILLIAM CLIBURN
Mississippi Southern College, Hattiesburg

The ranges of certain snakes in Mississippi as given in the current check list (Schmidt, 1953), and in general references (Klauber, 1956; Wright and Wright, 1957) require modifications, as discussed below.

Schmidt does not include Mississippi in the ranges of the following forms: *Natrix septemvittata, Natrix sipedon fasciata, Storeria occipitomaculata obscura, Heterodon simus, Abastor erythrogrammus,* and *Coluber constrictor priapus. Sistrurus miliarius streckeri* occurs in "Western Mississippi . . . ," *Natrix sipedon pleuralis* is listed for "northern Mississippi . . . ," *Natrix sipedon confluens* is credited to ". . . extreme western . . . Mississippi," and *Pituophis melanoleucus lodingi* is recorded from "Harrison County, Mississippi."

Actually, all of these snakes occur in the state, and the ranges of the last three have been previously extended (Cook, 1943; Conant, 1956; Cliburn, 1957).

The ranges of the following forms according to Wright and Wright (*loc. cit.*) also require discussion: *Elaphe guttata, Farancia abacura reinwardti, Haldea striatula, Lampropeltis doliata doliata, Natrix grahami, Natrix taxispilota taxispilota, Natrix taxispilota rhombifera, Rhadinea flavilata, Thamnophis sauritus, Tantilla coronata coronata, Abastor erythrogrammus, Coluber constrictor priapus, Natrix septemvittata, Pituophis melanoleucus lodingi,* and *Storeria occipitomaculata obscura.*

Natrix grahami Baird and Girard.—The Wrights do not list this species for Mississippi. Cook records it in the following counties: Carroll (1), Chickasaw (1), Coahoma (3), Holmes (1), Lauderdale (1), Sunflower (9) and Warren (2). The collection of Mississippi Southern College contains specimens from Bolivar and Sunflower counties.

Natrix septemvittata Say.—Cook reports three specimens: Lauderdale (2) and Forrest (1) counties. These records extend the range in eastern Mississippi southward from that of Wright and Wright. A female from Lauderdale County measures 25.5 inches in total length and 5.3 inches in tail length. It contains 15 embryos.

Examination of this specimen revealed that the two ventral dark stripes are vestigial; the stripes are limited to the neck region and occur toward the lateral margins of the ventral plates, rather than along the mid-venter. The rest of the venter is immaculate slate gray (in formaldehyde). All scale rows are keeled.

Scale counts and measurements are as follows: subcaudals, 82; ventrals, 135; ratio of subcaudals/ventrals, .603; scale rows, 19; supralabials, 7-7; infralabials, 10-10; postoculars, 2-2; preoculars, 2-2; anterior temporals, 1-1; posterior temporals, 2-2; ratio of tail length/-total length, .206.

Natrix taxispilota taxispilota Holbrook.—A specimen previously reported (Cook, 1943; Cliburn, 1956) from Adams County is 70 miles west of the range shown in Wright and Wright.

Natrix taxispilota rhombifera Hallowell.—Wright and Wright map this subspecies along the Mississippi River and in southwest and southeast Mississippi, and coastal Alabama. According to Cook, it is found statewide and is recorded from the following counties which are outside the range defined by Wright and Wright: Carroll (4), Chickasaw (6), Holmes (3), Lafayette (3), Lauderdale (4), Lee (11), Lowndes (3), Monroe (1), Oktibbeha (4), Pontotoc (1), Prentiss (2), Tishomingo (2), and Wayne (3). Cliburn (1956) reports it from Rankin (4) and Wayne (1) counties, Mississippi, and from Perry (4), Tuscaloosa (1), and Greene (1) counties, Alabama.

Natrix sipedon fasciata Linnaeus.—Reported from Harrison County (Allen, 1932). Cook gives the range in the state as "The western and southern parts of the state and in Lowndes and Lauderdale Counties." Cliburn (1957) records this subspecies from Jackson (3), Stone (1), Harrison (6), and Hancock (7) counties, and lists scale counts and other data. The Mississippi form varies considerably from more easterly *fasciata,* as pointed out in that paper.

Natrix sipedon pleuralis Cope.—Previously reported (Cliburn, 1957) as follows: Stone (1), Forrest (11), Perry (3), Wayne (2) counties. Additional county records are from Copiah (2), Lamar (2), Pike (6), Forrest (14), Perry (9), Covington (2), Amite (1), Greene-Perry (3), Jones (1), and Lawrence (1). I have seen this form taken in great numbers from Pearl River in Lawrence County by Mr. Donald Spence, a professional collector of Monticello, Mississippi.

Natrix sipedon confluens Blanchard.—Reported from Wayne and Lauderdale counties (Cook, 1943). Cliburn (1957) records it from Forrest County. None of these localities is in western Mississippi.

Storeria occipitomaculata obscura Trapido.—Separated by us from *S. o. occipitomaculata* by the following key character: *S. o. obscura* has a light cervical ring, 2 scales in width; in *S. o. occipitomaculata* the ring is replaced by three light spots. On this basis, specimens from southeast Mississippi are *obscura.* Wright and Wright indicate Mississippi to be in the range of *S. o. occipitomaculata,* with intergrades of the two forms in Jackson and George counties. Mississippi Southern College has specimens from Stone (1), Forrest (6), Lamar (1), and Perry (1) counties.

Thamnophis sauritus Linnaeus.—Not shown in the southern two-thirds of Mississippi by Wright and Wright. Approximately 70 specimens from this area in the Mississippi Southern College collection extend the range to the coast: Jackson (6), Harrison (1), Hancock (19), Stone (1), Perry (4), Forrest (14), Lamar (9), Walthall (1), Pike (1), Lincoln (2), and Copiah (1) counties.

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area for the species, and Lauderdale (5), Lee (17), Lowndes (1), Oktibbeha (10), and Pontotoc (2) counties, which are well outside their range. Mississippi Southern has specimens from Madison, Rankin, and Simpson counties.

Heterodon simus Linnaeus.—Cook lists four specimens, two from Stone County, and two from Pearl River County. Allen records one from Harrison County and three from Jackson County. A Mississippi Southern specimen was collected four miles southwest of Brooklyn, which extends the range of this form into Forrest County.

Rhadinea flavilata Cope.—Wright and Wright indicate the existence of this form in coastal Mississippi (panhandle region). Mississippi Southern has specimens which extend the range northward into Forrest County.

Abastor erythrogrammus Latreille.—Cook reports seven specimens: Pearl River (3), Copiah (1), Lowndes (2), Oktibbeha (1) counties. Three additional specimens are now reported: Stone County (1) and Forrest County (2). Wright and Wright show this form in southeast Mississippi only; Copiah, Lowndes, and Oktibbeha are not in southeast Mississippi.

Farancia abacura Holbrook.—Cook reports this snake from Lee (5) and Tishomingo (1) counties, which are in northeast Mississippi, outside the range given by Wright and Wright.

Coluber constrictor priapus Dunn and Wood.—Both Schmidt and Wright and Wright give peninsular Florida as the range of this subspecies. Six specimens of *constrictor* from Forrest County were identified by Mr. Walter Auffenberg as *priapus*. Smith and List (1955) allocate all Mississippi *Coluber* to this subspecies, but state that snakes from Bolivar and Washington counties (in the Delta region) are quite distinct from coastal specimens. It is assumed that specimens from southeast Mississippi belong to this form. Mississippi Southern College has specimens from the following counties: Jackson (8), Harrison (2), Hancock (14), George (1), Stone (1), Pearl River (1), Greene (1), Perry (3), Forrest (18), Lamar (4), Marion (2), Walthall (1), Pike (1), Wilkinson (1), Covington (1), Lincoln (1), Wayne (1), and Copiah (3).

Elaphe guttata guttata Linnaeus.—Wright and Wright do not include this form in the Mississippi Delta region, nor in southwest Mississippi. Cook records it from Adams (1) and Lafayette (2) counties, neither of which falls within the mapped range. I have seen 2 specimens DOR in Lafayette County.

Pituophis melanoleucus lodingi Blanchard.—As indicated by Conant (1956), this snake occurs in Forrest, George, Lauderdale, Perry, and Wayne counties. Although Cook reports that in July, 1940, this form was seen more often than any other snake in Perry County, and rural people of this area are familiar with it both by name and characteristics, collectors have rarely encountered it. It has been observed in west Lamar County by a farmer who described the snake to me. He has not seen it in many years. Wright and Wright show it

in Jackson and George counties. The range is not limited to Harrison County, as indicated by Schmidt (1953).

Lampropeltis doliata doliata Linnaeus.—Shown in extreme southeast Mississippi on the map of Wright and Wright. Cook records it from Adams (2), Jones (3), Lauderdale (2), Oktibbeha (1), Pike (2), Rankin (1), Sunflower (2), and Wayne (2) counties, a much broader range for this species than Wright and Wright indicate.

Tantilla coronata coronata Baird and Girard.—Recorded by the Wrights in the eastern one-third and in the coastal region of Mississippi. Cook lists it from the following counties west of this range: Lafayette (4), Lincoln (1), and Warren (1).

Sistrurus miliarius streckeri Gloyd.—Klauber lists the range as follows: "From the Pearl River Valley of southern Mississippi and southeastern Louisiana (where it intergrades with *S. m. barbouri*), north and west through Mississippi. . . ." His map indicates *barbouri* (but not *streckeri*) to occur in coastal Mississippi.

A specimen from Lincoln County, another from Amite County, and two from Copiah County all fall within the mapped range of *streckeri*. Mississippi Southern College has specimens from Forrest (1), Stone (1), and Hancock (1) counties.

Crotalus horridus atricaudatus Latreille.—Listed by Klauber (1956) as being "present in the area." The Mississippi Southern College Collection contains specimens from Lawrence (1), Adams (1), Warren (1), and Marion (1) counties.

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Relative Abundance of Twelve Southeastern Mammals in Six Vegetative Types[1]

STURGIS McKEEVER
University of California, Davis

In the southeastern upper coastal plain, agricultural practices and vegetative succession on abandoned land produce six vegetative types; namely, cultivated areas, tall weeds-broomsedge, pine, pine-hardwoods, upland hardwoods, and bottomland hardwoods. Agriculture produces pastures, meadows, fields of small grain, corn, cotton, peanuts, and tobacco. The type of agriculture and proportion of land in these crops varies in different areas and is dependent upon physiography, soil, and climate. In general, two or more crops usually occur on a limited area so that all cultivated areas may be grouped into a single vegetative type.

Succession on abandoned fields is similar to that described by Wells (1928) for the coastal plain of North Carolina. The stages are: tall weeds, broomsedge, pine, pine-hardwoods, and upland hardwoods. The first two stages may be grouped into a single tall weeds-broomsedge type, since they produce a similar life form, and species from each stage usually are present in the other. In some areas, either soil or land-use practices may produce what is essentially a pine climax, so that the last two stages of succession do not occur.

In bottomlands and poorly-drained areas, the vegetation consists of bottomland hardwoods; this type is self-perpetuating.

Plant species in the various types vary from one locality to another, but the life form of a given type is approximately the same in all localities. Pitelka (1941) demonstrated that life form of vegetation is the controlling factor in distribution of birds within the major biotic communities, and McKeever (1956) found vegetative life form a dominant factor controlling the distribution of many mammals.

Mammalogists who have studied southeastern mammals frequently mention the vegetative type in which a given species of mammal is most abundant, but the study of gray fox populations by Wood *et al.* (1958) apparently is the only one which deals quantitatively with any of the larger forms. This paper reports the results of a 21-month study of the larger mammals (deer and bear excluded) in eleven counties of southwestern Georgia and northwestern Florida.

Methods

All animals were collected with No. 2 coil-spring fox traps which were set at 0.1 mile intervals along service roads on farms, private shooting preserves, or forests of 3,000 to 12,000 acres in size. One

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[1] Field investigations were conducted while the author was employed by the U. S. Public Health Service.

hundred to 125 traps were set on Monday of each week and maintained until Friday; most areas were trapped for two consecutive weeks, or eight nights. All traps were baited on Monday and Wednesday with a mixture of fox and wildcat urine, skunk scent, and glycerine. In the event of rain, all traps were rebaited the following day.

Each trap was numbered and the type of surrounding vegetation recorded. Classification of the vegetation was based upon the subjective judgment of the writer. In many instances, traps were set at the edge of two types; these traps were assigned to the type with the greatest area.

Animals were removed daily and the species and trap number recorded. The number of sprung traps was recorded and the number of trap nights for each vegetative type was computed from the number of traps set less the number sprung. Percentage catch, here used as an expression of relative abundance, was computed for each vegetative type from the number of trap nights and number of animals caught over the 21-month period.

RESULTS

From September 20, 1955 to June 21, 1957, census lines were maintained on 48 randomly distributed areas and 2,688 mammals were collected in 31,145 trap nights. In order of decreasing abundance, the species represented were as follows: opposum, *Didelphis marsupialis;* raccoon, *Procyon lotor;* striped skunk, *Mephitis mephitis;* cottontail rabbit, *Sylvilagus floridanus;* gray fox, *Urocyon cinereoargenteus;* wildcat, *Felis rufa;* fox squirrel, *Sciurus nigra;* house cat, *Felis domestica;* red fox, *Vulpes fulva;* spotted skunk, *Spilogale putorius;* marsh rabbit, *Sylvilagus palustris;* and otter, *Lutra canadensis.* Distribution of the individuals of each species among the vegetative types is shown in TABLE I.

All species known to occur in the region and subject to census by the method used are represented except the weasel and gray squirrel. No specimens of the former species were taken; despite their obvious abundance, only two gray squirrels were caught and these were not tabulated. Three species were represented by ten or less individuals but were tabulated because they were believed to occur in that proportion. Although it is not a native mammal, the house cat was included because feral individuals of this species are an important component of the mammalian fauna, particularly on shooting preserves.

Percentage catch for each species in the various vegetative types is presented in Figure 1 with $\pm$ 2 SE plotted to show significance at the 5 percent confidence level. Numerical percentages $\pm$ 1 SE are given in TABLE I. Nine of the twelve species were significantly more abundant in their preferred habitat. The number of types in which the relative abundance of a species differed significantly from populations in all other types was as follows: five for the opossum, raccoon, and striped skunk; four for the cottontail rabbit and wildcat; two for the gray fox and house cat; and one for the marsh rabbit and fox squir-

TABLE I.—Distribution of twelve species of mammals in six vegetative types in southwestern Georgia and northwestern Florida

	VEGETATIVE TYPE						
SPECIES	Cultivated areas	Tall weeds-broomsedge	Pine	Pine-hardwoods	Upland hardwoods	Bottomland hardwoods	TOTAL
Opossum	49 (1.928±0.194)	468 (2.365±0.007)	30 (1.431±0.021)	117 (3.411±0.017)	7 (1.532±0.046)	93 (3.283±0.018)	764 (2.453±0.006)
Cottontail rabbit	39 (1.535±0.019)	221 (1.117±0.007)	12 (0.573±0.022)	41 (1.195±0.017)	5 (1.094±0.047)	24 (0.847±0.018)	342 (1.098±0.006)
Marsh rabbit	—	3 (0.015±0.007)	—	1 (0.029±0.017)	—	4 (0.142±0.019)	8 (0.026±0.006)
Fox squirrel	3 (0.118±0.063)	57 (0.288±0.007)	8 (0.382±0.021)	5 (0.146±0.017)	1 (0.219±0.047)	2 (0.071±0.019)	76 (0.244±0.006)
Gray fox	28 (1.102±0.011)	105 (0.531±0.007)	4 (0.191±0.022)	13 (0.378±0.017)	5 (1.094±0.047)	5 (0.176±0.059)	160 (0.514±0.006)
Red fox	10 (0.394±0.020)	16 (0.081±0.007)	2 (0.095±0.022)	—	—	—	28 (0.090±0.006)
Raccoon	65 (2.558±0.020)	490 (2.476±0.007)	16 (0.763±0.022)	76 (2.216±0.017)	11 (2.407±0.046)	90 (3.177±0.018)	748 (2.402±0.006)
Striped skunk	36 (1.417±0.019)	235 (1.187±0.007)	33 (1.574±0.022)	78 (2.274±0.017)	5 (1.094±0.047)	16 (0.565±0.019)	403 (1.294±0.006)
Spotted skunk	2 (0.079±0.020)	5 (0.025±0.007)	—	1 (0.029±0.017)	—	2 (0.071±0.019)	10 (0.032±0.006)
Otter	—	1 (0.005±0.007)	—	1 (0.029±0.017)	—	—	2 (0.006±0.005)
Wildcat	1 (0.039±0.020)	22 (0.111±0.007)	18 (0.861±0.022)	34 (0.991±0.022)	4 (0.875±0.017)	21 (0.741±0.019)	100 (0.321±0.006)
House cat	13 (0.512±0.020)	24 (0.121±0.007)	5 (0.239±0.022)	5 (0.146±0.017)	—	—	47 (0.151± 0.006)
TOTAL	246 (9.681±0.019)	1,647 (8.323±0.007)	128 (6.107±0.021)	372 (10.845±0.016)	38 (8.315±0.045)	257 (9.072±0.018)	(8.630±0.005) 2,688
Number of trap nights	2,541	19,788	2,096	3,430	457	2,833	31,145

Percentage catch ± 1 standard error is shown in parentheses

rel. Populations of the spotted skunk and otter did not differ significantly among the various types.

Since all traps were mechanically spaced at regular intervals, the number of trap nights in each type reflects its relative area (TABLE I), even though there was a high degree of interspersion of types. On many areas the vegetation was manipulated so as to maintain a large quail population, an interest best served by maintaining a large proportion of the areas in the early stages of plant succession (Stoddard, 1931). Therefore, more than half the trap nights were in the tall weeds-broomsedge type.

All types differed significantly from each other in relative abundance of the total mammalian population except tall weeds-broomsedge and upland hardwoods. In order of decreasing percentage catch of all species, the types were ranged as follows: pine-hardwoods, cultivated areas, bottomland hardwoods, tall weeds-broomsedge, upland hardwoods, and pine.

DISCUSSION

Since there was a high degree of dispersion among vegetative types, individuals of all species probably range over several types in their

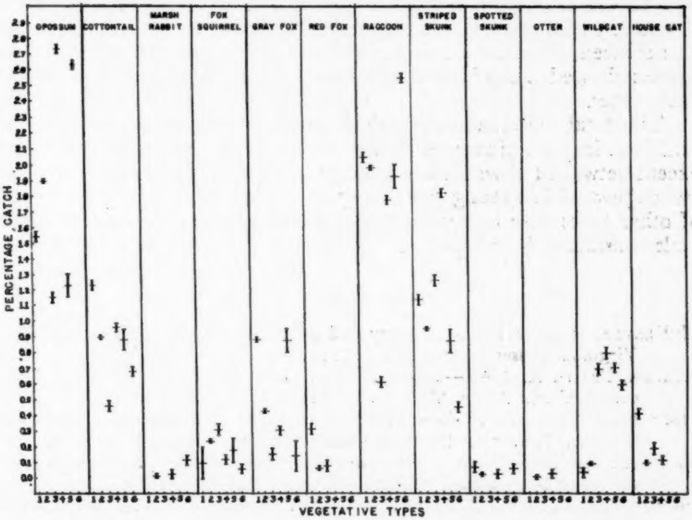

Fig. 1.—Percentage catch of mammals in six types of vegetation in southwestern Georgia and northwestern Florida. Median horizontal line represents computed percentage; vertical line represents ± 2 standard errors. Vegetative types are: 1, cultivated areas; 2, tall weeds-broomsedge; 3, pine; 4, pine-hardwoods; 5, upland hardwoods; and 6, bottomland hardwoods.

daily wanderings. The influence of a preferred habitat adjacent to one less desirable cannot be disregarded, but the number of trap nights in each type was considered sufficiently large to show habitat preference of the various species.

At present, three related land-use objectives are establishing a trend toward reduction or dispersion of types and increasing the acreage of the pine type. These objectives are: (1) reduction of crop land acreage by planting pine, (2) acquisition of additional land by pulp companies and conversion of all suitable areas to pine forests, and (3) reduction of hardwoods in all existing mixed stands in order to increase the volume of pine. The mammalian population of the region may, therefore, be expected to decrease in proportion to the degree to which the foregoing objectives are attained. Only the fox squirrel was most abundant in pine woods, and under intensive silviculture its numbers probably would decrease there because scattered hardwoods and overmature pines which now serve as den trees would be removed.

Summary

From September 20, 1955 to June 21, 1957, mammals were collected with No. 2 coil-spring fox traps on 48 areas in 11 counties of southwestern Georgia and northwestern Florida. In 31,145 trap nights, 2,688 individuals representing 12 species were trapped. Relative abundance of each species in six vegetative types was computed. Nine species showed a significant preference for one vegetative type, and six species showed a significantly different relative abundance in four or more types.

The total mammalian population was greatest in pine-hardwoods and least in pure pine, and showed a significant variation in all types except between tall weeds-broomsedge and upland hardwoods. Present trends toward increasing the acreage occupied by pine at the expense of other types may be expected to reduce the population of all mammals considered in this paper.

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Some Studies on Crayfish Distribution in a Small Pond

GEORGE CAMOUGIS[1] AND
JOSEPH K. HICHAR[2]

Harvard Biological Laboratories, Cambridge 38, Massachusetts

While trapping crayfish of the species *Orconectes virilis* Hagen (formerly *Cambarus virilis* Hagen; Hobbs, 1942) during the summer of 1956 in a small pond in Lincoln, Massachusetts, it was noted that certain sites within the pond yielded more crayfish than others. Also it was noted that the catches varied from time to time throughout the summer. These observations prompted speculations about the preference of the crayfish for certain sites in the pond, possible migration, and their population density. Therefore, it was decided to plan the trapping activities for the summer of 1957 to include a study of some of these problems.

Method

The site of the study was an overflow basin of the Hobbs Brook Reservoir in Lincoln, Massachusetts. Physically the basin approximates a rectangle about 180 m long in the east-west direction and about 45 m wide in the north-south direction. The average depth of the water is about 1.5 m when filled. The water level fell from about 0.5 m below normal level at the beginning to about 0.9 m below normal by the end of the experiments. The east and west ends are lined with large rocks which normally extend under the surface of the water. The sides are lined with gravel, the bottom of the south side being muddy in comparison to the somewhat more sandy bottom of the north side. Three stations were used in the studies. Station A was located in the middle of the east end (Fig. 1). Station B was located on the north side about 38 m west of the east end. Station C was similarly located on the south side, directly across from Station B.

Crayfish were trapped, marked, and released at these three stations. Minnow traps baited with fish trimmings were used to trap the crayfish. Haddock heads seemed to be the most effective bait. Salmon and haddock backs were less effective and mackerel heads least of all. The traps were placed approximately 7 to 8 m off shore at each station within a radius of about 2 m. Four experiments were carried out (Table I). In Experiment I the animals were trapped at Station A and released at Stations B and C. In Experiment II the

[1] Present address: Department of Biology, Clark University, Worcester 10, Massachusetts

[2] Present address: Department of Zoology, Ohio Wesleyan University, Delaware, Ohio

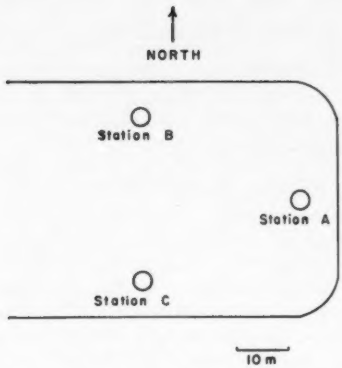

Fig. 1.—Diagram of station sites in one end of the pond.

animals were trapped at Stations B and C and released from the same stations from which caught. In Experiment III the crayfish were caught at Stations B and C and released at Station A. Finally in Experiment IV the crayfish were caught, marked, and released at Station A. In each experiment 100 marked animals were used, with the exception of Experiment II where 50 animals were returned to Station B but because of insufficient animals only 40 were released at Station C. After the initial trapping, marking, and releasing, the secondary

TABLE I.—Stations and numbers of animals involved in the initial and secondary trappings

Experiment	Station of Initial Trapping	Marked Animals Released Station	Marked Animals Released Number	Secondary Trapping Station	Secondary Trapping Markings A	Secondary Trapping Markings B	Secondary Trapping Markings C	Secondary Trapping Total	Percent Marked
I	A	B	50	A	—	6	14	94	21.3
		C	50	B	—	11	8	89	21.4
				C	—	1	6	36	19.4
II	B	B	50	A	—	6	4	113	8.8
	C	C	40	B	—	3	3	94	6.4
				C	—	2	6	50	16.0
III	B	A	100	A	—	12	7	95	20.0
	C			B	—	6	1	98	7.1
				C	—	2	3	38	13.2
IV	A	A	100	A	12	—	—	104	11.5
				B	12	—	—	152	7.9
				C	5	—	—	59	8.5
				Totals	29	49	52	1022	12.7

trappings in each experiment took place with three traps at each of the three stations for simultaneous sampling of the results of the experiments. The traps were first set for each experiment in the evening between 6 and 8 p.m., D.S.T. The following morning, about 12 to 14 hours later, the traps were removed and the crayfish were counted. Then 100 animals were marked and released at the appropriate stations. For identification the crayfish were marked on various structures with bright red fingernail polish. The evening of the following day, 34 to 36 hours later, the secondary trappings were carried out. The next morning the animals were collected from the traps and brought to the laboratory where they were counted.

RESULTS

The results are shown in TABLE I. The column on initial trappings shows the stations from which the crayfish were initially caught. The next column shows the numbers of crayfish that were then marked and released at the various stations. The data for secondary trappings show the number of marked animals that were recaught plus the total (including unmarked) animals caught at each of the three stations. "Markings" in the secondary trapping column refer to the places where the marked animals were released in Experiment I, where they were initially caught and subsequently released in Experiment II, where they were initially caught in Experiment III, and finally where they were initially caught and released in Experiment IV.

DISCUSSION

The experimental data show that marked animals were always caught at all three stations, no matter where they were initially caught or where they were subsequently released. Moreover, although the total numbers of crayfish caught at each station varied, the percentages of the total marked animals caught at each station usually had much less variation. It appears that these animals do not have a small, confined home range area but move freely about the bottom of the area of the pond that was tested. It is possible that the experimental area was too small geographically to detect a home range. Perhaps a home range, if it exists, is in the order of hundreds of feet or more. It is of interest that the crayfish did not give any evidence of territorialism. Many aquatic animals show territorialism in which they actively defend a small area (Davis, 1949).

At first sight it might be argued that the animals may have a small range but they are unable to migrate directly back after they are caught and released elsewhere. Experiment IV would argue against this being the case because the crayfish were caught, marked, and released at Station A. With the second trapping at the three stations, the percentages of marked animals out of the total caught showed very little variation. These data would tend to support a hypothesis that the marked animals moved freely about and distributed them-

selves evenly throughout the total population of the end of the pond under study. Other evidence that crayfish may distribute themselves randomly comes from a study reviewed by Penn (1950) in which a depopulated area of a stream yielded 6,070 crayfish per acre two days later.

It is interesting to note that the crayfish could move for linear distances of at least 30-40 meters between the various stations. Since crayfish are most active at night (Roberts, 1944; Hichar, unpublished data) the greater parts of these distances were probably covered during about 20 hours. Although this doesn't compare with the much greater distances reported to be covered by the Bermuda spiny lobster (Creaser and Travis, 1950), it does show that crayfish can effectively move around in a pond for appreciable distances.

Assuming that the marked crayfish became randomly distributed among the total crayfish population in the area sampled, if there were no differential survival between marked and unmarked animals, then a population estimate can be made. Animals marked with fingernail polish were kept in laboratory tanks for weeks without any apparent toxic effects. It is possible that the bright fingernail polish on various anatomical structures may have had a detrimental survival effect because of interference with natural protective coloration. This effect cannot be estimated. Assuming random distribution and equal survival, the percentage of total animals that were marked appears sufficiently large (12.7%) to allow the population of the sampled area to be estimated by the mathematical relationship used for estimating populations in similar studies (Lagler, 1956). The computed population is 3,066 animals. The experimental area was approximately 1,500 square meters or 0.37 acre. The population density was therefore about 8,300 crayfish per acre. These figures are in satisfactory agreement with those of other studies of crayfish standing crop reviewed by Penn (1950).

It is also of interest to note that the numbers of crayfish caught at Station C were consistently less than at the other stations. The substrate at station C was more muddy and appeared to have fewer stones than the other stations. Crayfish prefer to hide among niches in a rocky substrate (Roberts, 1944). Fewer crayfish may have been caught at Station C because the area did not offer as much protection. However, the data do not permit a conclusion that the marked crayfish tended to avoid Station C as compared to Stations A and B. Perhaps if longer periods of time were allowed to expire between releasing and secondary trapping, different distributions may have resulted. Also, since the crayfish can readily cover the distances between stations, the secondary trappings may not have represented samples of populations right at each station, but rather chance samplings of a population continually moving about the end of the pond under study. Results from future experiments involving larger test areas with greater distances between stations and a variety of time intervals between releasing and retrapping would be of great interest.

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Phytosociology of the Lowland Forests of Northern Wisconsin[1]

E. M. CHRISTENSEN,[2] J. J. (JONES) CLAUSEN,[3]
AND J. T. CURTIS

University of Wisconsin, Madison

The forests of northern Wisconsin may be divided for study purposes into two topographic types—the upland forests and the lowland forests. The composition and floristic relationships of the upland forests have been described by Brown and Curtis (1952). The present study is concerned with the second type, with the forests which are found on poorly drained sites which receive runoff waters from adjacent uplands or which are subjected in other ways to temporary or permanent high levels of soil moisture. Such sites are a prominent feature of the heavily glaciated terrain in northern Wisconsin. They are found in partially filled lake basins, along stream terraces, or on flat lands of glacio-lacustrine origin. They support forests which vary from stands of pure conifers in the wettest situations to stands of nearly pure hardwoods on the most mesic sites. The substrate in these lowland forests is rich in organic matter, frequently in the form of peat which may be present in beds many feet in thickness. The climate of the area is the Type I of Bochert (1950); it is characterized by cold snowy winters, reliable summer rains, and low rates of evaporation. The snow cover is usually deep enough to protect the soils from frost penetration to any great depth and often prevents any freezing of the soil. Cold air drainage into the lowland forest basins serves to increase the severity of the temperature microclimate and may result in frost on any day of the year.

The importance of these lowland forests is greater than their areal extent might indicate. Perhaps less than 10 percent of the land area in northern Wisconsin is occupied by them, but they have received far less disturbance than any of the upland types. Their direct economic potential as sources of lumber or other forest products is low, but they are of great importance in stabilizing the water supply of the region. Their role in providing wintering grounds for the white-tailed deer is also of high significance in the over-all conservation program (Christensen, 1954).

Few ecological investigations of the lowland forests have been made

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[2] Present address: Brigham Young University, Provo, Utah.

[3] Present address: University of Minnesota, Minneapolis.

in Wisconsin in the past. H. H. T. Jackson (1914) described the plant communities and their successional relations in his study of the vertebrate animals of a bog forest in Oneida County. He divided the forest into two types, one dominated by *Larix laricina* and *Picea mariana*, with some *Pinus banksiana* and *Sorbus americana* and an understory of bog shrubs, and the other dominated by *Thuja occidentalis* and *Abies balsamea* in its early stages and by *Tsuga canadensis*, *Picea glauca*, and *Acer saccharum* in its later phases, with an understory of *Nemopanthus mucronata*, *Amelanchier* sp. and *Acer spicatum*.

Similar accounts have been given for the bog forests of Michigan and Minnesota by Gates (1942), Conway (1949), and others. The regional pattern is unusually uniform, with wide-spread agreement that *Larix laricina* is the first tree to invade the ericaceous shrub stage of the open bog. This is followed by *Picea mariana*. The two exist in varying mixture in a quasi-stable forest community of potentially great duration. At some later time, following changes whose exact nature is in doubt, the *Larix-Picea* forest is replaced by a more shade-tolerant forest dominated by *Thuja occidentalis*, often with *Abies balsamea* and *Fraxinus nigra*. Information is neither so plentiful nor so uniform regarding the terminal stages of these lowland forests, though some type of hardwood forest, often with *Tsuga canadensis* as a prominent member, seems to be indicated.

The present study is an attempt to describe the full range of forest types found on lowland sites in northern Wisconsin and to relate them to similar forests in neighboring states. It is based on an examination of 108 stands in 21 counties, largely made by E. M. Christensen (1954) and J. J. (Jones) Clausen (1955). Certain additional information was obtained from the work of R. Ward (1956), R. T. Brown (1951), and H. N. Goder (1955). We wish to express our appreciation to them for this information and to Professor Grant Cottam for aid and advice throughout the study.

METHODS

The stands used in the study were all at least 15 acres in size, were located on lowland sites with a water supply in excess of that provided by rainfall, and were free from serious disturbance during the lifetime of the existing dominant trees. The last criterion needs some enlargement, as the problems faced were different than those usually met with elsewhere. It was easy to find stands which were totally free of direct human interference in the form of logging, drainage, or flooding. The major disturbance factor was a result of the use of many lowland forests as yards by overwintering herds of white-tailed deer. The trampling and browsing conditions approached those of a barnyard in many areas. Such stands were studied in a separate phase of the investigation (Christensen, 1954), but none of the stands in the present study were classed as true deer yards, since they showed evidence of only light utilization by deer.

Within each stand selected for study, the trees were examined by

one of the point methods, either the random pairs or the quarter method (Cottam and Curtis, 1949, 1956). The resulting data for 80 trees per stand included absolute values for density, dominance, and frequency. Relative values were obtained by dividing individual absolute values by the sum of values for each measure. The relative values for all three measures were combined by summation into a single importance value (IV) as described by Curtis and McIntosh (1951). The understory plants were sampled by means of quarter milacre quadrats at 20 points in each stand, with resulting data expressed as simple frequency. Presence lists were also made of all species in the stand, whether or not they occurred in the quadrats.

Specimens of most taxa encountered in the study are on file in the herbarium of the University of Wisconsin. Carices were identified through the gracious aid of Dr. James Zimmerman. Nomenclature in this paper follows that of Gleason (1952).

RESULTS

The examination of interstand relationships when data are available for many stands is best done by means of an ordination (Goodall, 1954). A variety of methods are available for the construction of such an ordination. The stands may be arranged by their degree of floristic similarity, by the joint occurrences of their major species, by a gradient based upon a quantitative measure of the species present multiplied by a behavioral index of the species, by factoral analyses, or by other means. These methods are discussed in full by Greig-Smith (1957) and will not be described in detail here. Suffice it to say that the simplest method of obtaining a preliminary ordination is that of the weighted behavioral index (Whittaker, 1954). When this technique is applied to forests, such as those of the present investigation, it is convenient to base the initial ordination on the trees only. For this purpose, it is necessary to know the amount of each species of tree in each stand, and the relative behavior of each species in respect to some factor gradient present in the stands. The amounts are available in the present case as importance values. The behaviors must be approximated from knowledge of the occurrence and growth of the species under the full range of site conditions which are represented in the study.

In the case of similar ordinational studies of Wisconsin upland forest communities (Curtis and McIntosh, 1951; Brown and Curtis, 1952) the major factor gradient has been the moisture supply at the site. The most important species were clearly arranged in a series from those growing best in dry soils to those growing best in mesic soils. The exact arrangement of the species in this series was determined by an examination of their joint occurrence, using the method of leading dominants.

For the northern lowlands forests, it appeared that a similar approach could be used, since prior studies by other investigators had indicated a series of species, from *Larix* to *Acer,* which was correlated

with decreasing moisture. Christensen (1954) used the leading dominant method on the data from many of the stands in the present study, especially those from medium-wet to mesic sites, and found the order of the species to be *Larix laricina, Picea mariana, Thuja occidentalis, Abies balsamea, Fraxinus nigra, Ulmus americana, Betula lutea, Acer rubrum, Tsuga canadensis, Fagus grandifolia,* and *Acer saccharum.*

Clausen (1957) studied another group of stands, with emphasis on those in very wet sites. She prepared an ordination based on the groundlayer species only, using a modification of Gleason's coefficient of similarity developed by Bray (1955). The coefficient was based on the frequency value for the groundlayer plants and resulted in an ordination of stands such that stands most nearly similar to each other were close together on a linear gradient, while stands which differed in composition were more remote. When the measured amounts of the trees in each stand were plotted against this non-tree gradient the species were found to be in a series: *Larix laricina, Picea mariana, Pinus banksiana, Thuja occidentalis, Abies balsamea, Fraxinus nigra, Betula lutea* and *Tsuga canadensis.*

By combining the data and results of the studies of Christensen and Clausen with additional information on more nearly mesic stands from the investigations of Brown (1951), Goder (1955) and Ward (1956), it was possible to arrange all of the tree species of the lowland forests of northern Wisconsin into a single order. Index numbers showing positions in this order, called adaptation numbers, were assigned to each species in an arbitrary range, 1.0 for the species in the wettest place (*Larix laricina*) to 10.0 for the most mesic place (*Fagus grandifolia* and *Acer saccharum*). The complete list is given in Table I.

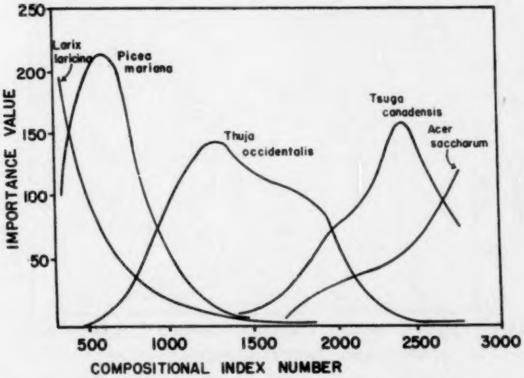

Fig. 1.—Importance values of five major tree species in relation to the compositional index numbers of stands in which they occur.

A compositional index for a given stand was obtained by multiplying the importance values for each species in the stand by the adaptation number of each species and summing the products. The indices could range from 300 for pure stands of *Larix* to 3000 for pure stands of *Fagus* or *Acer* or pure mixtures of these two. Such compositional indices were calculated for each stand in the study and the stands were then arranged in the order of their index number. In this way, the measured amounts of any component species or any environmental factor could be plotted against the compositional gradient. This has been done in Figure 1 for the major tree species. It is not surprising that the resulting curves are arranged as they are, since these species were most influential in determining the basic order. However, the lesser tree species in Figure 2 show similar patterns, although their values contributed but little to the order. The best indications of the nature of interstand relationship are given in Figure 3 and 4 which portray the changes in presence of various groundlayer species of differing behavior, plotted against a tree-based compositional gradient, in the construction of which they played no part.

More detailed information on the trees and groundlayer plants is given in Tables I and II, which show simple numerical averages of measured values according to 5 equal divisions of the gradient. As can be seen, there are no groups of species with similar distributional patterns, such as would be expected if discrete communities were present. Rather there is a continuous series of species, of varying amplitude which have optima at all possible positions along the gradient, forming a vegetational continuum.

A more detailed description of the species combinations to be found

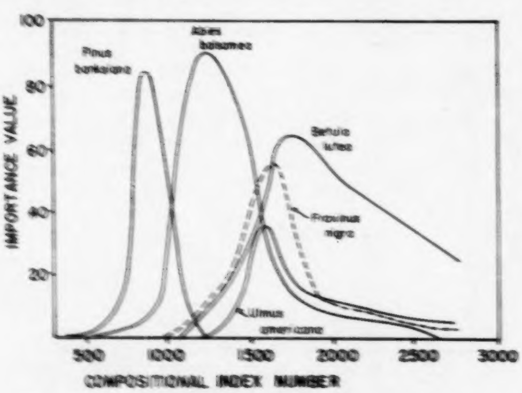

Fig. 2.—Importance values of five lesser tree species in relation to the compositional numbers of the stands in which they occur.

on the northern lowlands is most easily given according to consecutive segments of the compositional gradient. These segments must be arbitrarily delimited, since the flora as a whole shows no external evidence of discrete breaks which could be used to determine objectively the units. For purposes of this paper, the forests have been divided into three groups. The first of these, with compositional index numbers from 300 to about 700, includes most of the tamarack-spruce bogs, while the second, from 800 to about 1900, contains the cedar swamps and the black ash swamps. The third group, above 2000 on the index, is much less homogeneous. It comprises the so-called hardwood swamps, with yellow birch, hemlock and sugar maple as important trees. In the following discussions, the three segments will be treated separately with an interpretation of their stability, dynamics, and variants.

ORDINATION SEGMENT 300-700

The common trees of importance here are *Larix laricina* and *Picea mariana*. The groundlayer is rich in shrubs, particularly ericads, including species of *Andromeda, Chamaedaphne, Kalmia, Ledum,* and *Vaccinium. Pinus strobus* is present in many of the stands, but it rarely reaches a position of dominance. Other trees are *Thuja occidentalis, Abies balsamea, Populus tremuloides* and *Betula papyrifera,* all of which are infrequent. The herbaceous plants include many species which are typical of the open bog community, such as *Drosera rotundifolia, Sarracenia purpurea, Carex oligosperma, Carex trisperma, Eriophorum spissum,* and *Menyanthes trifoliata,* but also encompass more typical forest plants, such as *Cypripedium acaule,*

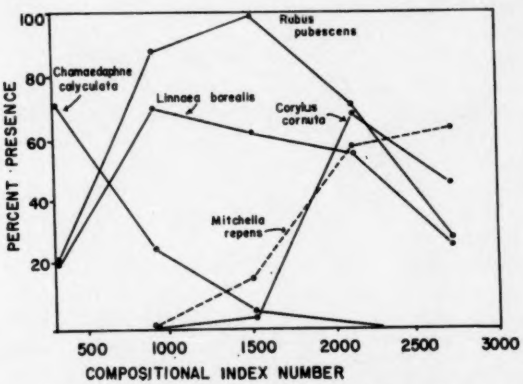

Fig. 3.—Percent presence (percent of all stands within an index class in which a given species occurs) in relation to the compositional index numbers of the stands in which they occur.

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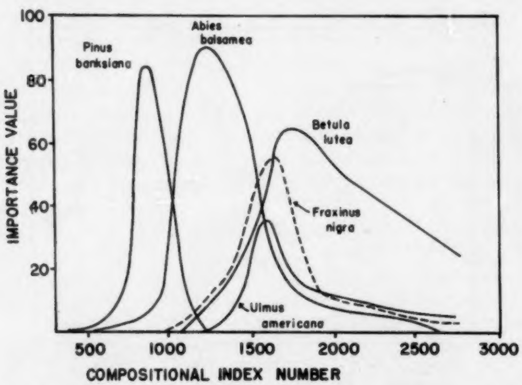

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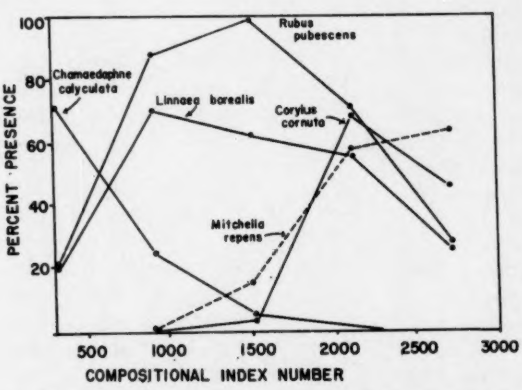

Fig. 3.—Percent presence (percent of all stands within an index class in which a given species occurs) in relation to the compositional index numbers of the stands in which they occur.

Gaultheria hispidula, Osmunda cinnamomea, and *Smilacina trifolia.*

The *Picea* bogs are typically found on moss peat derived largely from *Sphagnum* and *Polytrichum* species. Clausen (1957) found that the water-retaining capacity of the surface layers averaged 850 percent, while the pH was 4.5 or below. The peat showed reducing conditions, with occurrence of iron in the ferrous form. A separation of the peat into coarse, medium, and fine fractions by a sieving procedure showed that over 70 percent by weight was in the coarse fraction (too large to pass a 5 mm mesh sieve).

TABLE I.—Behavior of trees

Tree Species with Adaptation Numbers	Average Importance Value by Ordination Segments 300-799	800-1,299	1,300-1,799	1,800-2,299	2,300-3,000
Larix laricina (1.0)	**78.7**[1]	14.6	1.8	—	—
Picea mariana (2.0)	**193.7**	40.6	0.8	—	—
Pinus banksiana (3.0)	3.5	**31.6**	—	—	—
Pinus resinosa (3.5)	2.1	**2.7**	—	—	—
Populus tremuloides (3.5)	2.0	2.2	**2.6**	2.2	—
Pinus strobus (4.0)	**5.3**	0.7	1.0	**4.8**	1.1
Picea glauca (4.0)	0.5	**0.8**	1.7	**4.6**	0.6
Thuja occidentalis (4.0)	3.4	119.5	**122.7**	43.7	3.7
Prunus pennsylvanica (4.0)	—	—	—	0.2	0.2
Abies balsamea (4.5)	1.9	**63.0**	61.5	4.7	5.5
Populus balsamifera (4.5)	—	—	**1.6**	—	—
Populus grandidentata (5.0)	0.1	—	—	—	0.4
Betula papyrifera (5.0)	1.5	7.1	**12.7**	0.3	1.9
Fraxinus nigra (5.0)	0.1	6.6	**36.7**	11.7	3.6
Ulmus americana (5.5)	—	—	**19.3**	11.4	5.0
Acer rubrum (6.0)	0.1	1.0	6.3	**21.6**	7.3
Acer spicatum (6.0)	—	—	—	—	0.3
Quercus borealis (7.0)	—	—	—	6.3	3.6
Fraxinus americana (7.0)	—	—	0.6	0.3	**4.1**
Betula lutea (7.5)	—	3.0	33.7	**42.6**	35.9
Ulmus rubra (8.0)	—	—	**0.8**	6.2	0.8
Carya cordiformis (8.0)	—	—	—	0.2	—
Juglans cinerea (8.0)	—	—	0.4	1.6	0.2
Tsuga canadensis (8.5)	—	1.0	6.9	**88.7**	**125.3**
Tilia americana (8.5)	—	—	1.3	4.9	**13.4**
Ostrya virginiana (9.5)	—	—	—	2.4	**3.4**
Fagus grandifolia (10.0)	—	—	—	3.4	**11.3**
Acer saccharum (10.0)	—	—	—	34.5	**69.9**

[1] Modal values in bold-face type.

Forests in this segment of the gradient in Wisconsin give many evidences of a high degree of stability, in the sense that they may occupy the same area for long periods of time with little tendency to change by successional processes to other forest types. Other investigators have reached similar conclusions (Le Barron, 1948; Bergman and Stallard, 1916).

This evidence for stability of the type does not mean that any particular stand maintains a constant composition. Rather, it implies a dynamic stability, with wide changes possible in the relative numerical abundance of *Larix* and *Picea* in a given stand, from almost pure *Larix* to almost pure *Picea* or any intermediate mixture of the two. *Larix* is subject to periodic destruction by the larch sawfly and the larch case-borer, while both *Larix and Picea* are readily destroyed by fire. LeBarron (1948) pointed out that *Picea* has particular ability to re-establish itself after fire occurs in the swamps of Minnesota, due to the nature of seed-scattering after a burn. Catenhusen (1950) came to the conclusion in studying bog forests of central Wisconsin that both *Larix* and *Picea* readily re-establish themselves after superficial fire, from any seed stock which escaped destruction. The proportions of the two major species in the stands following catastrophe naturally are likely to be very different than those existing before the destruction.

During drought years, surface fires may actually consume the top layer of the peat, which then becomes submerged following the return of normal water levels. This may cause the replacement of the bog forest by semi-open, park-like muskeg, by open sphagnum bog or even by a sedge bog dominated by both sphagnum and various sedges. The

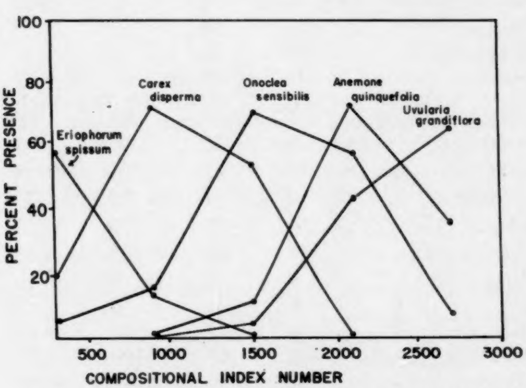

Fig. 4.—Percent presence of selected herb species in relation to the compositional index numbers of the stands in which they occur. See Table II for species not illustrated here.

TABLE II.—Behavior of understory species

Understory Species	Percent Presence by Ordination Segments 300-799	800-1,299	1,300-1,799	1,800-2,299	2,300-3,000
Eriophorum virginicum	**50**[1]	11	—	—	—
Eriophorum spissum	**58**	14	—	—	—
Andromeda glaucophylla	**64**	21	—	—	—
Chamaedaphne calyculata	**76**	25	—	—	—
Ledum groenlandicum	**82**	**82**	21	—	—
Smilacina trifolia	**82**	68	37	—	—
Vaccinium angustifolium	**58**	50	32	25	9
Polygonum sagittatum	8	**50**	16	—	—
Habenaria obtusata	6	**54**	32	—	—
Aster puniceus	12	**54**	37	—	—
Carex leptalea	6	**61**	47	—	—
Nemopanthus mucronata	36	**54**	26	—	—
Carex disperma	18	**71**	53	—	—
Vaccinium myrtilloides	72	**75**	16	—	—
Equisetum fluviatile	18	**50**	26	29	—
Ribes triste	10	**50**	47	29	—
Viola pallens	30	**82**	53	14	—
Dryopteris cristata	26	**71**	69	29	—
Lonicera canadensis	4	**64**	63	29	18
Coptis trifolia	28	**82**	79	43	36
Linnaea borealis	20	**71**	63	57	27
Carex trisperma	84	**89**	79	14	9
Gaultheria hispidula	70	**86**	47	57	18
Cornus canadensis	44	**93**	74	72	64
Caltha palustris	8	43	**53**	14	—
Glyceria striata	6	43	**74**	14	—
Alnus rugosa	42	89	**90**	14	—
Onoclea sensibilis	6	14	**69**	57	9
Impatiens biflora	10	39	**90**	29	18
Osmunda cinnamomea	44	64	**69**	43	9
Circaea alpina	4	46	**74**	43	55
Mitella nuda	8	64	**90**	43	27
Arisaema trifolium	4	7	**69**	57	64
Rubus pubescens	22	89	**100**	72	27
Galium triflorum	6	68	**90**	86	82
Maianthemum candense	32	86	**100**	86	**100**
Adiantum pedatum	—	—	**53**	14	27
Aralia nudicaulis	16	68	95	**100**	73

TABLE II.—(*continued*)

Understory Species	Percent Presence by Ordination Segments 300-1,299	800-1,299	1,300-1,799	1,800-2,299	2,300-3,000
Clintonia borealis	18	79	84	**86**	55
Oxalis acetosella	6	47	37	**57**	55
Streptosus roseus	2	21	26	**100**	82
Diervilla lonicera	2	11	26	**57**	27
Pteridium aquilinum	8	7	5	**72**	18
Oryzopsis asperifolia	—	—	5	**86**	55
Actaea alba	—	—	16	**57**	55
Anemone quinquefolia	—	—	16	**72**	36
Corylus cornuta	—	—	5	**72**	46
Trientalis borealis	42	86	84	86	**91**
Gymnocarpium dryopteris	6	64	74	57	**73**
Lycopodium lucidulum	4	18	16	57	**73**
Lonicera oblongifolia	6	18	11	57	**73**
Aster macrophyllus	4	39	44	—	**60**
Thelypteris phegopteris	—	21	42	43	**64**
Lycopodium obscurum	—	4	—	57	**82**
Polygonatum pubescens	—	4	21	43	**64**
Mitchella repens	—	—	11	50	**60**
Uvularia grandiflora	—	—	5	43	**64**
Trillium grandiflorum	—	—	16	14	**55**

[1] Modal values in bold-face type.

analysis of peat profiles frequently reveals an alternation of sedge peat, sphagnum peat and peat containing woody remains of *Larix* and *Picea,* clearly indicating past periods of retrogression from forest to non-forest communities. In other cases, the peat profiles show considerable unbroken deposits of woody peat of *Larix* and *Picea* origin, thus indicating long periods of relative stability of the type.

ORDINATION SEGMENT 800-1,700

This segment includes the type locally known as the cedar swamp, because of the prevalence of *Thuja occidentalis,* the so-called white cedar. In addition to *Thuja, Pinus banksiana, Abies balsamea, Betula papyrifera, Ulmus americana,* and *Fraxinus nigra* attain their optimum levels of importance in this segment. Groundlayer species which achieve their highest presence include *Moneses uniflora, Equisetum fluviatile, Nemopanthus mucronata, Carex leptalea, Viola pallens, Coptis trifolia,* and *Cornus canadensis* in the lower half of the segment and *Carex pedunculata, Caltha palustris, Onoclea sensibilis, Alnus*

rugosa, Mitella nuda, and *Rubus pubescens* in the upper half.

Variation in tree cover in this segment is greater than in the first. The major type and the one occupying the largest total area is that dominated by *Thuja occidentalis.* A rare type is that dominated by *Pinus banksiana,* found mostly in the northwestern part of the State. Toward the upper end of the segment are swamps with a high content of *Fraxinus nigra* or mixtures of that species and *Ulmus americana.* Either the *Thuja* or the *Fraxinus* swamps may occasionally have a high content of *Abies balsamea,* but the latter rarely reaches a position of leading dominance in any swamp.

The *Thuja* swamps are frequently found on coarse wood peat, although when considerable amounts of *Fraxinus nigra* and other hardwoods are present, the organic layer is more compacted and contains more fine particles of muck. Clausen (1957) found a considerable increase in soil nutrients in this segment as compared to the spruce bogs, particularly in available calcium, magnesium, and potassium. The water-retaining capacity averaged 500 percent, which was correlated with the decreased content of the coarse peat fraction (to 50%). In contrast to the moss peat bogs, Wilde and Randall (1951) found a "striking drop in acidity resulting from an increased supply of electrolytes; the frequent presence of free oxygen and a positive oxidation-reduction potential indicate that ground water of these sites is in a state of constant horizontal movement."

Like the *Larix-Picea* bogs, the *Thuja* swamps of Wisconsin often give indications of a high degree of stability. The explanation of this stability appears to lie in the nature of the reproduction of cedar, especially its vegetative reproduction.

Cooper (1911), Moore (1922), Harlow (1928), Curtis (1946), and Nelson (1951) have described various types of vegetative reproduction in white cedar. In the dynamics of white cedar swamp, these are very important. In Wisconsin, as elsewhere, windthrown and leaning trees are very common in cedar swamps. The root systems are very shallow, penetrating only a foot or two into the substratum. When a cedar tree tips over, a flat-bottomed basin several feet in diameter and usually only a few inches deep is formed. These depressions and the organic soil formed by criss-crossed fallen trunks make an extremely irregular forest floor.

The tipping-up process is very gradual and usually a large percentage of the root system remains in the soft substratum. When one of these trunks finally lies flat on the ground, numerous branches on the upper surface grow vertically and form a line of dense, vegetatively produced stems of various ages. This type of propagation has been described by Curtis (1946) in Maine and Nelson (1951) in Michigan. It has been called "layering from windthrow" by Nelson. In cedar swamps in Wisconsin, this process is perhaps of greatest importance in the maintenance of the stand. It is most commonly observed in stands with large trees and represented by all ages of individuals.

Branch layering is common in Wisconsin. As the lower branches

droop, they come in contact with the forest floor and produce adventitious roots. Nelson and Moore have observed some cases where the rapidly growing sphagnum bed had built upward and thus engulfed the branches. Under these conditions adventitious roots will form on the main trunk as well as on the lateral branches.

The studies in Maine by Curtis and in Michigan by Nelson indicate that the effective reproduction by vegetative propagation may be large in comparison with the number of plants established by seed. Little attempt was made in this study to distinguish between the specific numbers of stems produced by vegetative means and by sexual means, but general observations and some seedling data indicate that vegetative reproduction is of great importance in the continuation of the swamp stands. One of the notable features of white cedar stands is the large number of stems, both living and dead, in the two to four inch dbh size class. It is apparent that these stems are primarily the result of vegetative propagation. Vegetative reproduction is more tolerant to shade than seedling reproduction and the developing adventitious root systems of vegetatively developed stems coupled with the still somewhat active root system of the parent stem would insure against moisture deficiency.

Habeck (1958) has shown that *Thuja occidentalis* in Wisconsin consists of at least two ecotypes, one adapted to upland sites and the other to swamp conditions. It is not known whether the tendency toward vegetative reproduction noted in the cedar in the swamps of the present study is a special characteristic of the swamp ecotype or whether it is potentially present in the upland strain also. The closely related *Thuja plicata* reproduces extensively by branch layering and from fallen trees on upland sites in British Columbia (Schmidt, 1955).

Abies balsamea, the balsam fir, is the second important member of the cedar swamps, but only chance conditions make it possible to show temporary dominance. Its low growth rate, high mortality, short life, and shallow root system usually result in a combination of conditions that relegate it to a position of lesser importance than the dominant white cedar. Its high presence is doubtless due to its manner of reproduction. Young balsam trees and saplings commonly occur in dense clumps in Wisconsin swamps. These can be attributed to layer origin (Cooper, 1911; Moore, 1922; Roe, 1950). Balsam produces abundant seed and can germinate on moist humus and rotten logs according to Roe. When once established by seed, the subsequent increase of the clones can be rapid, judging from their form.

Toward the upper end of this ordination segment, hardwoods take over an increasing share of the dominance. Many of these sites are along stream valleys and are inundated with water during some period of the year. The soils tend to be fine wood peats or lacustrine mucks. Windthrow is not as common as in those swamps dominated by *Thuja,* but broken and rotten timber is frequently seen. The trees, except for an occasional large *Betula lutea, Pinus strobus,* or *Thuja occidentalis,* are relatively small. Conspicuous is the large number of saplings,

especially those of *Fraxinus nigra.* This species reaches greatest importance in areas which are inundated for much of the growing season. Associated with it are *Acer rubrum, Betula lutea,* and *Ulmus americana.* Vegetative reproduction is of minor importance in this segment, even in the case of *Thuja.* Sprouting, however, occurs in *Acer rubrum* and vegetative propagation may be of some significance in *Abies balsamea.*

The *Thuja-Abies-Fraxinus* swamps are clearly related to the *Larix-Picea* bog forests, as is shown by the gradual and continuous change in species combinations of the groundlayer plants. The mode of transition from one set of trees to the other, however, is not fully understood at the present time. In Shawano, Langlade, Forest, and Oconto Counties in the northeastern portion of the state, many large swamps are to be seen with an overstory of large and decadent trees of *Picea mariana* and a few *Larix laricina* under which there is a dense understory of young *Thuja occidentalis,* often mixed with *Abies* and *Fraxinus.* The succession here is quite clear and appears to be a typical case of autogenic change with replacement based on differential shade tolerance and moisture requirements. In the north central area of Vilas, Iron and Price Counties, such intermediate stands are rare. In the few instances observed (Clausen, 1957), *Thuja* was invading the *Larix-Picea* forests in a patchy or highly aggregated manner by vegetative layering from a few chance seedlings which had become established on logs or hummocks. The *Thuja* clumps greatly reduced the light intensity and caused the elimination of both *Larix* and *Picea* in their immediate vicinity. In the northwestern counties, intermediate stands are also of infrequent occurrence. Several instances are known where the conversion from *Picea* to *Thuja* took place in a single step following catastrophe. In these sites, alder thickets of *Alnus rugosa, Cornus stolonifera* and *Nemopanthus mucronata* had replaced old *Larix-Picea* stands after fire. A dense understory of *Thuja* of seedling origin developed under the shrubs and eventually overtopped them to give rise to nearly pure stands of *Thuja.* The reasons for these geographical differences in type and amount of successional conversion are not clear.

The majority of stands in this segment of the compositional gradient are found on sites with non-stagnant waters, as along streams, around springs, on the shores of large wind-swept lakes, or other places where water is free to move through the peat. Most such places have probably never been occupied by true bog forests of *Larix* and *Picea,* but were invaded directly by the cedar swamps, usually following an alder thicket community. Their peats are relatively shallow and their profiles frequently are of woody origin all the way down.

ORDINATION SEGMENT 2,000-2,700

The swamp hardwoods of this segment clearly approach the terminal forests of the uplands in composition. The most important trees are *Tsuga canadensis, Acer saccharum, Fagus grandifolia* (in north-

eastern Wisconsin), *Betula lutea,* and *Tilia americana,* with *Acer rubrum, Acer spicatum,* and *Ostrya virginiana,* as lesser members. All of these are found in the corresponding segment of the upland forest gradient (Brown and Curtis, 1952). Important groundlayer species include *Trientalis borealis, Lycopodium lucidulum, Polygonatum pubescens, Thelypteris phegopteris, Uvularia grandiflora, Trillium grandiflorum, Dirca palustris, Oxalis acetosella,* and *Streptopus roseus.*

The sites are rarely if ever exposed to prolonged inundation. Their high moisture content is due to a soil which is rich in organic matter, largely the result of peat decomposition, or to impeded internal drainage with an accompanying beta or gammagley layer in the soil profile. They may be found on extensive peat deposits of old bogs, along meandering streams, or in shallow, undrained depressions on the uplands.

Both *Tsuga canadensis* and *Betula lutea* reach their optimum development in Wisconsin in stands in the lower part of this segment. They once formed majestic forests over extensive areas on the poorly-drained lacustrine clays of the lowlands around Lake Superior and Lake Michigan. They also occurred in abundance in the riverine swamps of the Flambeau and other northern rivers, where they were accompanied by significant amounts of *Ulmus americana.* The forests of *Acer saccharum* and *Tilia americana* of the upper portions of the segment occur only on the most nearly mesic sites. They are presently of infrequent occurrence, being found chiefly in Iron, Forest, and Florence Counties. The stands with an admixture of *Fagus grandifolia* are restricted to the counties bordering on Green Bay and the northern Lake Michigan shore.

These terminal lowland forests so closely resemble the comparable forests of the mesic uplands as to be scarcely distinguishable in terms of overall composition. However, a few species reach significantly higher levels of presence in the lowland stands and may be viewed as indicators of the type. These include: *Circaea alpina* (55% P in lowlands, 30% P in uplands), *Gymnocarpium dryopteris* (73 vs. 24), *Thelypteris phegopteris* (64 vs. 30), *Lonicera oblongifolia* (73 vs. 48), *Lycopodium obscurum* (82 vs. 41), and *Oxalis acetosella* (55 vs. 22).

All of the hardwood swamps are relatively stable, with significant amounts of seedling reproduction of all of the major tree species. Vegetative reproduction is infrequent, except in *Tilia* and *Fagus* (Ward, 1958). There is a successional trend towards increased dominance by *Acer saccharum,* but this trend is usually halted by catastrophe as in the corresponding upland stands (Stearns, 1949). Outright destruction of the forest by cutting and burning frequently leads to invasion of *Acer rubrum, Betula papyrifera* or *Populus tremuloides.* Sometimes nearly pure stands of *Betula lutea* will seed into a burned area, but this rarely happens with any other of the original dominants.

SUMMARY

This paper presents a discussion of the lowland forests of northern Wisconsin based on phytosociological data from 108 stands. The substrates of these forests are subject to temporary or permanent high moisture content and are high in organic matter, often in the form of peat.

Frequency, density, and dominance were recorded for the trees in each stand: frequency was determined for understory plants. The relative frequency, density, and dominance of tree species were added, resulting in an importance value. This importance value was weighted by an adaptation value for the tree species. The sum of the weighted importance values for any stand was the compositional index number for this stand, and stands were arranged along a gradient in order of increasing index numbers. The behavior of individual species was then graphed according to this gradient.

Species were found to be arranged along this gradient in continuous sequence with no distinct groupings. The most important trees were *Larix laricina* and *Picea mariana* in the wettest, most acid sites, *Thuja occidentalis, Abies balsamea* and *Fraxinus nigra* on intermediate sites, and *Tsuga canadensis, Betula lutea* and *Acer saccharum* on the most nearly mesic, circumneutral sites. The characteristics of each of these three groupings are described in detail.

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Book Reviews

FISHES OF THE GREAT LAKES REGION (Rev. Ed.). By Carl L. Hubbs and Karl F. Lagler. Cranbrook Institute of Science, Bulletin No. 26. 227 pp., 251 figs. and 44 color plates. 1958. $5.00.

The revision of this well-known, widely used manual includes not only the expected up-dating of nomenclature, but also significant changes in format. Among the latter are a complete rearrangement (and moderate expansion) of the introductory material, a grouping of color plates in the front, and a vastly improved composition. Together they result in a more easily used and readable book.

The new introductory material includes a brief treatment of the physical features and productivity of the Great Lakes drainage basin and a short section on the zoogeography of the fish fauna. The discussion of post-glacial redispersal is revised in keeping with more recent knowledge of distributions and continuing change of the basin through the activity of man.

Nineteen new color plates (including suckers and shiners) will be welcomed by student and sportsman alike. Reproduction of color on the original plates is greatly improved. Of significance to the beginning student of fishes and the general biologist is the addition of a key to larval lampreys and the expansion of the references to embrace recent taxonomic studies.

Perhaps the only "regrettable" change is the increase of one-half inch in width, for which compensation is made by the addition of a flexible, but still water-proof, cover. Although increased in size, the Hubbs and Lagler manual will still fit (and ought to be) in the pockets of all who are interested in fish.—ROBERT E. GORDON, University of Notre Dame.

ALGAE. THE GRASS OF MANY WATERS. By Lewis Hanford Tiffany. Charles C. Thomas, Springfield, Ill. Second Edition xv, 199 pp., 41 pls., 12 figs., 4 tables. 1958. $6.50.

Those who have regretted that Professor Tiffany's 1938 book on the algae has been out of print will welcome this second edition. The new edition has kept completely to the form of the original and has an added chapter called *Algae and Research.* In this new chapter, Tiffany has reviewed the work of the past twenty years not only "on" the algae, but also in part "with" the algae. The new chapter is unfortunately only seven pages in length and many significant researches have been slighted or not reviewed at all. There is for example no treatment of the subject of heterotrophy in algae or their use as assay organisms for vitamins. The number of general references listed has been reduced from 25 to 22. Of this last number only nine have appeared since 1938. Almost no changes have been made in the plates and figures; one of two colored plates in the original edition is now in black and white, and the second has been replaced by a diagram indicating the Antarctic food chain. The new edition remains at least as useful as the original, and I find myself in substantial agreement with Theodor Just, who reviewed the first edition here, (American Midland Naturalist 21:265-266, 1939). The second edition is "a good exposition of the intricate physiology and ecology of the algae." It is a valuable and interesting treatment that succeeds in the compromise it offers between what is palatable and what is technically correct.—RICHARD J. BENOIT, University of Notre Dame.

AN INTRODUCTION TO THE PLANT KINGDOM. By Norman H. Russell. The C. V. Mosby Company, St. Louis. 353 pp. 184 illustrations. 1958. $5.50.

In the recent Golden Jubilee Volume of the Botanical Society of America the accomplishments and progress in various fields of botany were acclaimed in articles by distinguished botanists. The views of those who wrote the articles dealing with botanical education were notably less sanguine. Donald Peattie in one entitled "On the Popularization of Botany," implied that botany is not popular and that its academic practitioners are not without blame. Two other articles dealing specifically with the teaching of college botany suggest by their titles "College Botany Could Come Alive" and "The Odor of Botany" that botany is moribund and not entirely fragrant in the nostrils of our students. If these views properly evaluate the state of botanical teaching the advent of a textbook declaring in its preface that the author "must please as well as educate," is a matter of interest to those concerned with the teaching of botany, particularly in the introductory courses.

Mr. Peattie in the article mentioned above states, "The author of a textbook is under no compulsion to make his book interesting or to make students feel that they would like to go on with the subject." The trend in current textbooks, however, seems to be an attempt to combine the essential of accurate communication of biological information with eye appeal in the format and whatever literary charm the author can muster, in order to make the book interesting.

Dr. Russell, Professor of Biology at Grinnell College, takes cognizance of this aim in his preface and introduction, and rightly points out the intellectual and aesthetic aspects of plant science which have charmed generations of botanists. There will, however, be those who will take issue with his dictum that "Only the method of science is essentially dry and dull."

The book is designed for a one-semester elementary course based upon the plant kingdom approach. Encyclopedic coverage is not attempted, the type method of selected species or genera being used throughout. These, for the most part, include familiar representatives which have appeared in many textbooks although some old favorites are absent. It seems to this reviewer unfortunate that none of the motile unicellular or colonial green algae have been included among the types, since they hold much interest for the student as well as representing the primitive type and an important evolutionary tendency to which the author alludes.

Following a brief introductory section on nomenclature, classification and evolution the book is arranged in five parts on algae, fungi, mosses and liverworts, lower vascular plants (through gymnosperms) and higher vascular plants. The classification used is modern, although it is doubtful that it has been accepted by the majority of botanists as the author suggests. Only one of four other recent botanical texts examined uses the same classification throughout and it seems preferable to recognize that classification of the higher taxa is in a period of flux. The inclusion of a chapter on the "Ecology of Algae" and another on "The Fungi and Man" are most desirable additions and the author uses these to add material to capture student interest. They might well be expanded and others added in future editions. If this reviewer's reaction is any index of Dr. Russell's success in writing a textbook with more than ordinary ability to please and intrigue his students that success stems from these chapters. The section on angiosperms includes a very brief outline of the root, stem and leaf and a review of important families of flowering plants.

The descriptions of the taxa represented are brief and the author has attempted to "write on the students level." This requires some elimination of detail but the coverage is generally accurate with a notable exception in which

chlorophyll is said to be the only pigment found in the green algae, no accessory pigments being present. The photographs are excellent but the diagrams are oversimplified and show little detail. A glossary is included.

As Dr. Russell remarks, this type of textbook is out of fashion, although this book along with the recent volumes of Haupt and Bold may indicate the resurgence of evolutionary approach to the study of plants. Certainly many of the leaders in the so-called modern fields of botany were weaned on just such old fashioned stuff and there is no reason why an evolutionary framework, not devoted slavishly to analysis of life histories but liberally representing the wealth of interest to be found in plants of all groups, should fail to compete for student interest.

This book is best adapted to teaching students who have had some prior introduction to biological concepts. — Robert P. McIntosh, University of Notre Dame, Notre Dame, Indiana.

Plant Breeding and Cytogenetics. By Fred C. Elliott. McGraw-Hill Book Company, New York City, New York. 395 pp. 1958. $8.50.

Anyone who attempts in an up-to-date way to interrelate two such large fields of endeavor as plant breeding and cytogenetics is certainly a brave soul. The old system of two separate disciplines is certainly much simpler to administrate and less controversial. However, we all realize if we ever had an example where two areas needed to be unified, this is most emphatically one. The unification of these two fields has been well done by the author of this textbook. Not only is the book excellent for individuals directly involved in such courses, but it will be useful as a reference book for any professional person whose subject matter in teaching crosses the two fields.

From the student's standpoint, in order to obtain the greatest benefit from studying the book, an elementary knowledge of genetics and cytogenetics is necessary. Some knowledge of plant anatomy, physiology and perhaps plant pathology is prerequisite. The author, realizing that the background accomplishments in subject-matter areas does vary considerably among students, has at the proper places worked background material into the text, without, in most cases, diluting the interest of the person who has had more than the minimum training in the various areas under discussion.

For those who would use this as a reference book, it has two things to offer. First, it includes a great deal of valuable information which has been collected from numerous sources and secondly the bibliographical references included in the text and at the end of the chapters are extensive and up-to-date. This aspect alone makes this a valuable book for the more advanced student.

The areas in which fundamental knowledge is lacking are pointed out and presented as a challenge to future participants in the area of plant breeding, rather than as a deterring factor.

In general this book should play an important role in the training of future plant breeders. Basic information is needed by the student in order to get the maximum good out of the book, and additional information will be necessary to make him a finished product. Between these two ends the user will receive from this book an understanding of, appreciation for and training in this large division of plant science.—Alvin V. Beatty, Professor of Biology, Emory University, Atlanta, Georgia.

TEXTBOOK OF DENDROLOGY (4th ed.). By William M. Harlow and Ellwood S. Harrar. McGraw-Hill Book Company, New York, New York. xi + 561 pp., 236 figs. and 67 plates (maps). 1958. $8.75.

Well known and widely accepted in previous editions, the fourth has some important additions and changes. The distribution maps for *Pinus lambertiana* and *P. contorta,* a discussion of taxonomic entities and nomenclature, a list of state trees, and 12 more titles in the bibliography are among the new features. *Larix alaskensis* included in the previous edition is wisely omitted. All distribution maps have been redrawn and improved although minor readjustments are still necessary, e.g., *Pinus strobus* occurs in Mexico. Halftone illustrations are generally better, although an occasional one (Fig. 82, *Abies magnifica*) is not as good as it was in the third edition. The nomenclature has been brought more in line with Little's checklist; for example, yellow birch is called *Betula alleghaniensis,* and pecan, *Carya illinoensis.* However, in contrast to Little, he considers *Carya ovalis* as distinct from *C. glabra.* Although Fig. 9 showing twig growth is confusing as a result of calling the last year's increment the "1st year," errors in general are minor. In view of its increasing importance as a weed tree in the southeastern United States, the empress tree, *Paulownia tomentosa,* might have been included. The net result, however, is a still better textbook which will continue to be accepted as the leader in its field.—A. J. Sharp, The University of Tennessee.

QUANTITATIVE PLANT ECOLOGY. By P. Greig-Smith. Academic Press Inc., New York. 198 pp. Illus., 1957. $6.00.

In a recent symposium one of the speakers pointedly emphasized the striking contrast in certain studies between the scrupulously accurate measures and techniques used in describing individual organisms, species populations, or physical environment and the cavalier description often accorded the vegetational milieu. Quantitative techniques of sampling and analysis of vegetation now available and being developed are not as widely and effectively used by ecologists and other field biologists as they might be, in spite of the rapid expansion of effective tools for this purpose.

Dr. Greig-Smith, of the University of North Wales, has made available a valuable volume bringing together a description of the various techniques of quantitative sampling and statistical analysis now widely scattered in the extensive literature on the subject. Much of this material is only slightly touched on in most of the currently available textbooks of ecology and this book will be a necessary and welcome addition to the ecologists book shelf.

In seven brief chapters Dr. Greig-Smith considers: (1) quantitative methods of describing vegetation, (2) methods and problems of sampling, comparison of results and tests of significance, (3) pattern of species distribution, methods of determining and assessing random and non-random distributions, (4) relations among distribution patterns of species, (5) correlation between vegetation and environmental factors, (6) description and delineation of plant communities as related to classification of vegetation, (7) his views on the contributions of quantitative approach to ecological theory. Two brief appendices include a discussion of meterological data and species distribution and also several useful statistical tables.

The treatment is particularly useful to the non-mathematical biologist in outlining common methods at some length and in offering assessments of the values and limitations of various methods. His discussion of Raunkaiers "Law

of Frequency," which is still widely misinterpreted in current texts and articles is an example.

Dr. Greig-Smith warns of the pitfalls to which ecologists may be exposed in applying quantitative methods but emphasizes two important advantages gained by their use.

"(1). . .the detection and appreciation of smaller differences. (2). . .a sounder basis of judgment of the significance of differences observed." — ROBERT P. MCINTOSH, University of Notre Dame, Notre Dame, Indiana.

A HUNDRED YEARS OF EVOLUTION. By G. S. Carter; Sidgwick and Jackson, London. (Distributed by The Macmillan Company, New York.) 206 pp., 4 figs., 1957. $3.75.

This little book is one of the many that has been written to celebrate the centenary of Darwin's work. It is a useful addition to this extensive literature. The book should be interesting and informative for the large audience not primarily devoted to the study of evolutionary theory. Actually, all but the specialist can probably obtain new insight from the discussion of the scientific and intellectual milieu around the time of Darwin. Dr. Carter's stated objective is to review the development of the Darwinian theory at a time when it has become rather generally accepted by biologists. The historical approach has resulted in a clear, very readable account of this development. The book is divided into two sections dealing with the nineteenth and twentieth centuries respectively. The outline of the geological time-scale and glossary of scientific terms which end the work will be useful for some readers.

The six chapters dealing with the nineteenth century are extremely informative despite their conciseness. The advances in geology and evolutionary ideas prior to Darwin are lucidly discussed including not only obvious topics such as the work of Lyell and Lamarck but also the German Natur-philosophie of the time and Philip Gosse's *Omphalos*. After a chapter dealing with the life and work of Charles Darwin, interesting chapters are devoted to the reaction of the general public and of the biologists with a discussion of the later nineteenth century. For the reviewer the first half of the book was the more interesting.

The eight chapters dealing with the twentieth century are primarily concerned with the impact of the Mendelian rediscovery and subsequent developments on evolutionary thought. A chapter containing an elementary exposition of Mendel's experiments and interpretations seems superfluous for most people likely to read the book in this country. The controversy between the Mendelians and biometricians which led to the temporary demise of Darwinism is followed by chapters concerned with more recent advances in genetics and ecology. Discussions of micro- and macro-evolution and an excellent concluding section bring the book to a close. The conventional neo-Darwinian view is presented as being capable of providing a probable explanation of the facts of evolution and the author feels that the invocation of other principles, even in secondary roles, is unnecessary. Goldschmidt is not mentioned. The exposition of the neo-Darwinian concept is reasonable and clear.

In conclusion, Carter has provided a book that can be read profitably by almost any student of biology and by some students in other disciplines who are interested in evolution and the famous dispute over evolution in the last century. It would appear to offer a succinct, coherent picture of evolution for advanced undergraduate students and also for graduate students preparing for

general examinations. — G. E. GRAF, University of Notre Dame, Notre Dame, Indiana.

FIRST BOOK OF GRASSES. By Agnes Chase (Third Edition). Smithsonian Institution, Washington, D. C., xix + 127 pp., 94 figures, 1959. $3.00.

For nearly forty years American students of grasses have learned their first lessons in grass morphology from Mrs. Chase's excellent little volume. Twice it has been out of print and unavailable for considerable periods of time. We welcome the appearance of the third edition by the original author, who is now in her ninetieth year.

The First Book of Grasses is unique in being written as a textbook on grasses rather than as a taxonomic treatment of the Gramineae. The twelve chapters cover vegetative structures, inflorescences and spikelets, and the diverse types of grass spikelets. While the chapter titles do not so indicate, each chapter in general covers a single tribe or a closely related group of tribes. A summary and directions for study of spikelets follow each chapter. The work is copiously illustrated with Mrs. Chase's fine line drawings of grass structures. A diagrammatic summary of twelve principal grass tribes of the United States follows the body of the text. The nomenclature here and throughout the work follows that of Hitchock's Manual of the Grasses of the United States. An interesting decorative touch is the inclusion of a colored reproduction of Albrecht Dürer's "Das grosse Rasenstück" as frontispiece.

The present work is largely a reprint of the earlier editions with very few changes. The classification of the grass family is presently in a state of great change, with new arrangements being suggested frequently. Many of these changes are based upon studies in genetics, cytology, morphology of embryos, vasculation, epidermal cells, response to chemicals, manner of germination, and other characters. At some later time, it might be appropriate to include a discussion of these matters in an introductory guide of this sort, and to indicate the outlines of the proposed newer systems of classification.—RICHARD W. POHL. Curator of the Herbarium, Dept. of Botany, Iowa State University, Ames, Iowa.

COMPARATIVE MORPHOLOGY OF VASCULAR PLANTS. By A. S. Foster and E. M. Gifford. W. H. Freeman and Company, San Francisco, Calif., 555 pages, 1959. $9.00.

This, the most recent textbook on the comparative morphology of the vascular plants will be welcomed as one of the clearest introductions to the vast body of knowledge on this subject. The selection of the material and the presentation of the basic facts of plant morphology reflect the large amount of experience accumulated by the authors in both research and teaching.

This textbook is clearly written for the student with a background of the fundamentals in this subject. It is intended for a one-semester course but, in my estimation, could well serve, with additional reference assignments to source material, for a one-year course in plant morphology. The addition of a glossary might even more enhance the usefulness of the text. There are 19 chapters, each of appropriate length, in a total of 555 pages. The first six chapters serve to orient and to refresh the student's mind on the basic morphological features and the general plan of the vascular plant as well as to outline the anatomy and organography of the sporophyte and its reproduction. There follows a splendid discussion of the major groups, both living and fossil, with the designation of

"Tracheophyta" to characterize the vascular plant divisions of the plant kingdom.

The classification to delimit the major divisions is the time-tested one of *Psilopsida, Lycopsida, Sphenopsida* and *Pteropsida* — so aptly and admirably presented in an older and classic text on this same subject. Incorporated in the text is a considerable amount of paleobotanical information — well chosen to support the principles discussed — but never detracting from the subject matter. In this respect, the authors have the knack of epitomizing succinctly the salient features and characteristics of major groups, wisely omitting the details of individual differences between organisms.

Throughout, the text is well illustrated with excellent photographs, photomicrographs, well-chosen drawings and diagrams; these incorporate illustrations of some of the more recent research on embryogeny and morphogenesis. Each chapter closes with a bibliography of the important references cited. The latter, although purported not to be complete, do include the most authoritative references on the subjects discussed. Further, the bibliography is printed in two columns to a page, thus making each item cited stand out and very easy to read. For clarity, each topic within a chapter is introduced in bold face and the scientific names of plants are italicized throughout, although a bold face printing of the latter also might profitably be included in a subsequent printing.

This modern and most needed text in the comparative morphology of the vascular plants is well written and the printing is large and easily read. I believe that the authors have presented a superb textbook incorporating as it does some of the most recent research in morphogenesis and evolution. The result is a substantial teachable book which should receive wide adoption and go through several printings. — ALBERT L. DELISLE, Sacramento State College, Sacramento, California.

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Style, arrangement, spelling, and abbreviations should conform to the usage of recent numbers of this journal. Do not underline any words except scientific names. Acknowledgments can be included in the Introduction, or may be offered as a footnote attached to the title of the article. Papers should be concisely written. A subsidy will be required for papers which exceed twenty journal pages in length.

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